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ON THE COVER – Shells of the genera *Musculium* and *Sphaerium*. Illustrations by John L. Tottenham.

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A COMPARATIVE STUDY OF DISTRIBUTIONS OF THE MUDWHELKS *TEREBRALIA SULCATA* AND *T. PALUSTRIS* IN A MANGROVE SWAMP IN NORTHWESTERN AUSTRALIA

Fred E. Wells

ABSTRACT

The distribution of the mudwhelks *Terebralia palustris* and *T. sulcata* were compared in a small mangrove swamp in the Bay of Rest, North-West Cape, Western Australia. *T. sulcata* was widely distributed in the swamp while *T. palustris* was restricted to a small area in the north. In the area where the two species overlapped, *T. palustris* occurred higher on the shore and in finer sediment than did *T. sulcata.*

INTRODUCTION

Mangrove swamps are among the dominant intertidal habitats of many tropical marine areas, including the north coast of Western Australia (Semeniuk et al., 1978). The trees form dense swamps in the mid to upper tide levels of protected bays and estuaries. Molluscs of mangrove areas were originally thought to be unique to the swamps, but more recent studies have shown that there are few species which live only in mangroves; most also occur on adjacent muddy or rocky shores (Coomans, 1969). *Terebralia palustris* (Linnaeus) and *T. sulcata* (Born) are two of the few gastropods characteristically found in mangroves, where they live on the mud surface or crawl up the pneumatophores of *Avicennia marina* (Forskal). *T. palustris* is common throughout the tropical Pacific and *T. sulcata* occurs from New Caledonia to the Indian Ocean (Cernohorsky, 1972). Both have been recorded in the northern Australian areas of Queensland and the Northern Territory (Saenger et al., 1977) and both are found also in Western Australia. Despite the wide geographic overlaps in the distributions of the two *Terebralia* species, I could only find one report of the two species occurring in the same mangrove swamp (Macnae, 1967). Macnae (1968) stated elsewhere that the two species are almost sympatric, but there is no published information available on the extent of their sympatry.

The present paper examined comparatively the distributions of *Terebralia palustris* and *T. sulcata* in a small mangrove swamp in the Bay of Rest, North-West Cape, Western Australia (22°18′S; 114°08′E). The Bay of Rest is a small, protected bay in Exmouth Gulf. It is 2 km wide at the mouth (Fig. 1) and has mangroves at the midtidal level of 1.4 to 2.1 m; the maximum tidal range is from 0.2 to 3.0 m. *Avicennia marina* and *Rhizophora stylosa* Griff. are the dominant mangroves; small numbers of *Ceriops tagal* (Pers.) also occur.

MATERIALS AND METHODS

Aerial photographs of the Bay of Rest were used to map the bay and the mangrove species present. A general survey of *Terebralia* was conducted in September 1979, during which 48 stations were examined (Fig. 1). Stations were 200 m apart, except in special circumstances (such as stations 20 and 21 which were in isolated mangrove stands). Samples were collected at stations in the seaward and landward margins of the mangroves. In some areas, the mangroves were not deep enough for two stations and only one was made. At each station, four 1 x 3 m quadrats were sampled 5 m apart. Each quadrat was searched for mudwhelks and all individuals found were counted.

A detailed examination of the small scale distribution of mudwhelks was made in the area of stations 1 to 3 (Fig. 1). Three transects 50 m apart were run through the entire mangrove zone from the sand-mud interface on the landward margin seaward to the lower limit of *Avicennia marina* pneumatophores.

A 2 x 2 m quadrat was searched every 10 m and all mudwhelks were identified and counted. All mudwhelks on transects 1 and 2 and all *Terebralia palustris* at stations 7 and 8 on transect 3 were measured to the nearest 1 mm. Stations were marked with wooden pegs and depths measured to the nearest 1 cm on a subsequent high tide. These depths were converted to absolute shore heights by comparing them with the tidal predictions for Learmonth, 5 km away (Anonymous, 1979).

A sediment sample of approximately 200 ml was removed from each station with a corer 4 cm in diameter. Samples were air dried in the field. Upon return to the laboratory, organic matter was removed by adding hydrogen peroxide daily until no further reaction occurred. Samples were washed and allowed to settle for 1-3 days before the supernatant water was drained. The sediment was dried to constant weight at 60°C, then sieved through a series of graded sieves with apertures of 1000, 500, 250, 125, and 63 μm. The material remaining on each sieve was weighed to 0.1 g and the weights converted to ϕ values on the Udder-Wentworth scale (Blatt et al., 1972). The scale ranges from one to five, with the smallest fraction (63 μm) having a value of five.

RESULTS

Terebralia sulcata was widely distributed in the Bay of Rest (Fig. 2), with individuals found in all areas except where *Rhizophora stylosa* was present. In some sections, such as stations 30-32, *R. stylosa* was the seaward mangrove tree, but pneumatophores of *Avicennia marina* extended onto the mudflat in front of the *R. stylosa*; *T. sulcata* occurred among the pneumatophores. Several areas of high density of *T. sulcata* were found (Fig. 2); the principal one was in the northern part of the bay at stations 1-3, where the detailed transects were made.

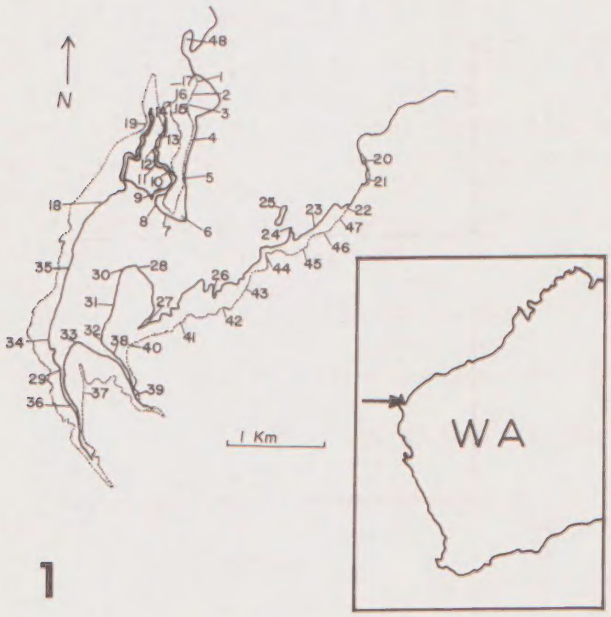
In comparison with the wide distribution of *Terebralia sulcata*, that of *T. palustris* was limited (Fig. 3). Isolated individuals were found among *Avicennia marina* at stations 14-16, 22 and 38. The only major concentration of this species was at stations 1-3. *T. palustris* was found in greatest densities in mud where water remains trapped at low tide, usually at the junction of the mud and a landward sand bank.

The detailed survey of stations 1-3 revealed that *Terebralia palustris* occurred from the upper limit of the mangroves at a shore level of 2.1 m down to 1.9 m; few individuals occurred below 1.9 m (Fig. 4). *T. sulcata* had the reverse pattern, occurring from the lower limit of the mangroves at 1.4 m to 1.8 m. Few individuals of this species occurred above 1.8 m. The two species also had different preferences for sediment grain size (Fig. 5). Densities of *T. palustris* were greatest in fine mud, while *T. sulcata* had its highest densities in coarser sediments. There was some overlap in the shore heights and sediment grain sizes utilized by the two species. An index of overlap (Horn, 1966) was calculated for all *T. palustris* and *T. sulcata* recorded on the three transects. The overlap in this area, where the two species occurred sympatrically, was 0.20.

Maturity in both species is indicated by a thickened lip of the shell aperture which is formed when the animal is full grown. Apertures of most individuals of *Terebralia sulcata* longer than 38 mm in shell length were thickened; *T. palustris* above 57 mm were thickened. The populations of both species on transects 1 and 2 were largely composed of individuals with thickened lips (Fig. 6). The mean size of *T. palustris* on these transects was 77.8 ± 7.5 mm, 1.6 times the mean size of *T. sulcata* (48.2 ± 1.2 mm). Few juveniles of *T. palustris* were found on transects 1 and 2, but most individuals at stations 6 to 8 on transect 3 were juveniles (Fig. 6), indicating that there is some migration of individuals during growth. No concentrations of juvenile *T. sulcata* were found in the Bay of Rest during the survey.

DISCUSSION

The statement of Macnae (1968) that *Terebralia palustris* and *T. sulcata* are almost sympatric has been demonstrated in the Bay of Rest. However, the two species had different distributions within the bay, possibly correlated with preferences for shore height and sediment



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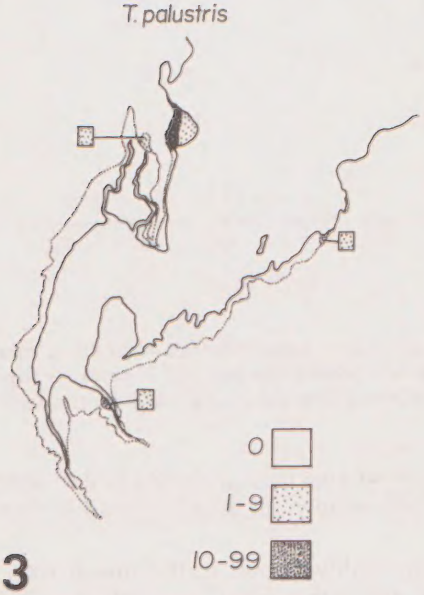

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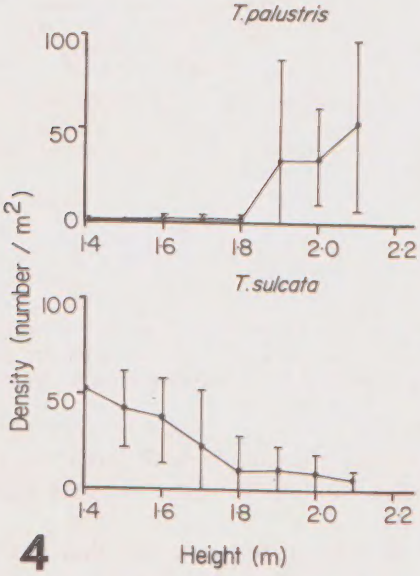

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FIG. 1. Map of the Bay of Rest showing the locations of the sample sites. FIG. 2. Distribution of *Terebralia sulcata* in the Bay of Rest in number of individuals per square meter. FIG. 3. Distribution of *T. palustris* in the Bay of Rest in number of individuals per square meter. FIG. 4. Densities of *T. palustris* and *T. sulcata* at various shore heights. The mean and one standard deviation are shown.

grain size. Potamidids are deposit feeders (Bishop, 1979) as are some cerithiids, which are in the same superfamily. Houbrick (1974) has demonstrated differential particle selection in

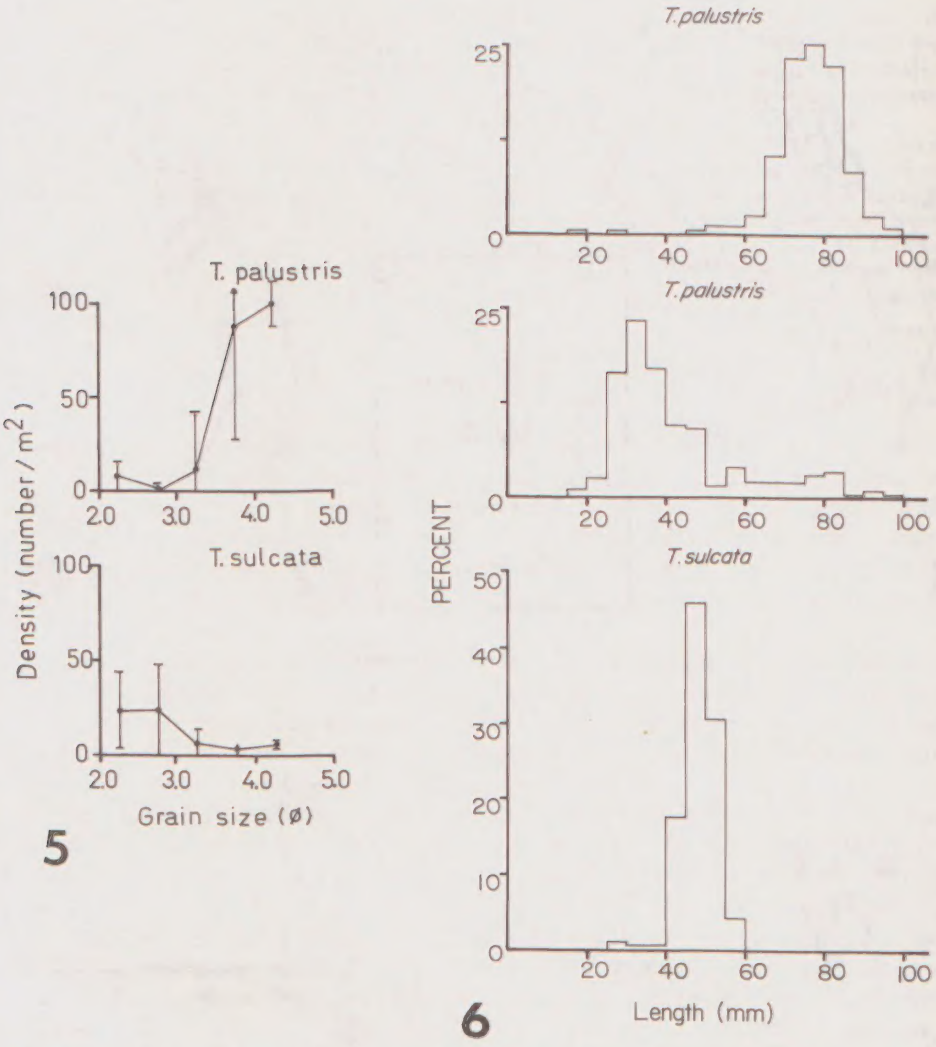

FIG. 5. Densities of *Terebralia palustris* and *T. sulcata* at various sediment grain sizes (in ϕ values). The mean and one standard deviation are shown. FIG. 6. Size-frequency diagrams of *T. palustris* (upper) and *T. sulcata* (lower) from transects 1 and 2 and *T. palustris* (center) from stations 6 to 8 on transect 3.

congeneric cerithiids of different sizes. The mean shell lengths of *T. palustris* and *T. sulcata* suggest that they utilize separate segments of the food supply, an area of possible further study.

Macnae (1968) reported that both species occur in shallow pools in the mangroves. In the Bay of Rest, *Terebralia palustris* definitely occupied this habitat, particularly where a sand bank abruptly met the mangrove mud. *T. sulcata* also occurred in shallow pools, but was more common in well-drained areas where there was no surface water. In Queensland, both species of *Terebralia* occur in the upper mangrove levels where *Bruguiera* and *Ceriops* are the dominant mangroves (Macnae, 1967; 1968); neither snail occurred in the soft mud of the *Rhizophora stylosa* forest. A similar pattern was shown in the Admiralty Gulf of Western Australia, where *T. sulcata* occurred in an upper *Ceriops* and *Aegialites* zone but not in the adjacent *Rhizophora* zone (Wells & Slack-Smith, 1980). Both species occurred among *Avicennia marina* in the Bay of Rest but not in *R. stylosa*.

The question as to why both species avoid *Rhizophora stylosa* has not been resolved, but there are several possible reasons. *R. stylosa* occurred from 1.4 to 2.1 m, the same shore heights occupied by the two *Terebralia* species in the Bay of Rest. In other mangrove areas where *R. stylosa* occupies a distinct shore level, the mangrove could occupy a different shore height than the two *Terebralia* species. The mud in which *R. stylosa* lives is fine grained with a high organic content. Small sediment grain size is unlikely to exclude *T. palustris*, which attained its highest densities in the finest sediments. Vermeij (1973) pointed out that anaerobic respiration in mangroves at lowtide creates acid conditions which are countered in molluscs by a variety of calcium carbonate conservation mechanisms. In potamidids, the portion of the shell in contact with the sediment is often eroded by the sediment acidity. Such erosion was encountered in both *Terebralia* species, but it was more pronounced in *T. palustris*, which lives in areas with a higher organic content. It is possible that the *R. stylosa* sediments, with their high levels of organic material, are too acidic for mudwhelks.

ACKNOWLEDGEMENTS

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PARTHENOGENESIS AND BIOCHEMICAL VARIATION IN SOUTHEASTERN *CAMPELOMA GENICULUM* (GASTROPODA: VIVIPARIDAE)

Alvan A. Karlin, Virginia A. Vail and William H. Heard

ABSTRACT

Adult individuals from six bisexual populations of *Campeloma geniculum*, one unisexual enclave of presumed *C. geniculum* and two enclaves of *C. parthenum* were surveyed for 20 electrophoretically detectable proteins. Incubating young from females of both bisexual and unisexual collections were analyzed for five proteins. The results indicate geographic regional differentiation in bisexual populations, and three clones of unisexuals were revealed. Results of mother-offspring analysis demonstrate sexual reproduction in bisexual populations and apomictic parthenogenesis in unisexual enclaves.

INTRODUCTION

Campeloma is the only viviparid gastropod genus known to contain both bisexual and parthenogenetic "species". For at least one species, *C. rufum*, apomictic parthenogenesis has been documented by cytological methods (Mattox, 1937), while apomictic parthenogenesis was inferred from biochemical data for *C. decisum* (Selander et al., 1977). Van der Schalie (1965) reported that parthenogens and bisexuals were distributed allopatrically, viz. that parthenogenetic *Campeloma* occurred only north of the Tennessee River system and bisexual *Campeloma* occurred only south of that system. Thus, the three southern species, *C. regularis, C. floridense* and *C. geniculum*, have been considered to be dioecious sexually reproducing species.

However, Vail (1979) recently recognized an unisexual enclave of *Campeloma* from within the geographic range of *C. geniculum*. Males and hermaphrodites were absent among more than 3000 individuals examined from this enclave, and Vail (1979) concluded that the snails were reproducing parthenogenetically and applied to these animals the name *C. parthenum*. Currently, three additional unisexual enclaves have been located within the distribution of bisexual *C. geniculum*. In this initial study, we used biochemical analysis of two of those unisexual enclaves and six bisexual populations to determine variation among both enclaves and populations and to determine the mode of reproduction in each.

MATERIAL EXAMINED

Between October 1979 and May 1980, a total of 111 adult *Campeloma geniculum* (Conrad) and 19 adult *C. parthenum* Vail were collected from eight localities in Florida (Fig. 1: sites 1-4 and 6-9; also see below) and one locality in Georgia (site 5). Samples from six sites (1-3 and 5-7) contained both males and females, whereas only females were found at sites 4, 8 and 9.

Bisexual populations

Site 1: Chipola River at State Road 167, 1.6 km N of Marianna, Jackson County (30°47′30″N x 85°12′00″W); 10♂♂, 10♀♀, 101 embryos. **Site 2:** Chipola River at Federal Highway 90, Marianna, Jackson County (30°46′15″N x 85°12′45″W); 2♂♂, 9♀♀. **Site 3:** Spring Creek at Federal Highway 90, 3.2 km SE of Marianna, Jackson County (30°45′45″N x 85°11′15″W); 10♂♂, 10♀♀, 63 embryos. **Site 5:** Flint River at State Road 32, about 19 km NE of Albany, Lee County (31°44′45″N x 84°00′15″W); 6♂♂, 14♀♀. (The type locality of *Campeloma geniculum* is the Flint River at Albany; no snails were found there.) **Site 6:** Ochlockonee River at Old Bainbridge Road, about 20 km NW of Tallahassee, Leon County (30°35′00″N x 84°22′45″W); 10♂♂, 10♀♀. **Site 7:** Ochlockonee River at Federal Highway 27, 17.6 km NW of Tallahassee, Leon County (30°15′15″N x 84°23′15″W); 5♂♂, 5♀♀.

Unisexual enclaves

Site 4: North Mosquito Creek adjacent to Florida State Hospital, Chattahoochee, Gadsden County (30°42'20"N x 84°51'30"W); 10♀♀, 76 embryos. **Site 8:** Lake Talquin (reservoir of the Ochlockonee River) at Coe's Landing, 20.8 km W of Tallahassee, Leon County (30°27'15"N x 84°29'00"W); 9♀♀. (These animals were topotypes of *Campeloma parthenum*.) **Site 9:** Little River at State Road 268, Gadsden County (30°31'00"N x 84°30'10"W); 10♀♀, 74 embryos.

METHODS

All animals were returned alive to the laboratory at Tall Timbers Research Station, where they were initially sexed by inspection of the tentacles (dimorphic in males, *fide* Vail, 1977) and then stored separately by sex in chilled spring water until processed for electrophoresis (not more than 72 hrs later).

Processing animals for electrophoresis entailed: mechanically deshelling individuals with the aid of pliers, examination for parasites (parasitized animals discarded), and confirmation of sex by inspection of the gonad. All young contained in females' pallial oviducts were removed and the brood was placed in a vial containing buffer (0.5 M Na_2HPO_4, pH 7.5), a code number corresponding to the female's number was placed on each vial, and the vials were stored at 0°C until used. No loss of enzymatic activity was noted for embryos stored in this manner. For adults, the entire animal was minced finely with the aid of a single edged razor, homogenized in an equal volume of buffer chilled to 4°C, and centrifuged at 25,000 g at 4°C for 60 min. The supernatant of water soluble proteins was then decanted and stored at 4°C overnight. Immediately prior to electrophoresis, embryos were individually crushed in wells on a spotting plate containing two drops of buffer. This suspension was stirred with a toothpick, absorbed onto filter paper wicks and the gels inoculated for electrophoresis.

The 20 cistrons coding for proteins studied were: catalase (CAT); general protein (GP); glucosephosphate isomerase (GPI); esterases (EST-1,2,3,4); l-leucyl-l-tyrosine peptidases (PEP-1,2); glucose-6-phosphate dehydrogenase (G-6-PDH); glyceraldehyde-3-phosphate dehydrogenase (G-3-PDH); malate dehydrogenases (MDH-1,2,3); α-glycerolphosphate dehydrogenase (α-GPDH); phosphoglucomutases (PGM-1,2); 6-phosphogluconate dehydrogenase (6-PGDH); isocitrate dehydrogenase (IDH); and superoxide dismutase (SOD).

The cistrons coding for proteins are represented by abbreviations. If several forms of the same protein are present and each is coded by an independent cistron, a hyphenated numeral serves to differentiate the cistrons. The protein with the greatest anodal migration is called 1, the next 2, and so on. Where electromorphic variation occurs, the electromorph (allele) with the greatest anodal migration is called a, the next b, and so on.

Techniques of horizontal starch gel electrophoresis and histochemical staining follow those described by Selander et al. (1971) and Selander et al. (1977), with the following modifications: CAT, GP, GPI, EST and PEP were visualized on the LiOH discontinuous ion system; G-6-PDH, G-3-PDH, MDH and α-GPDH were resolved on the Tris-citrate-EDTA, pH 7.2, counter-ion system; and 6-PGDH, PGM, IDH and SOD were scored on the phosphate-citrate ion system. For embryos, GPI, EST, IDH, α-GPDH and 6-PGDH were scored from the phosphate-citrate ion system (embryos examined only for EST were surveyed on the LiOH gel: see Results and Discussion below). All gels were 12.5% starch (Electrostarch Lot 307, Otto Hiller Electrostarch Co., Madison, Wisconsin, U.S.A.).

Genotype frequencies observed on the electropherograms were compared to those expected based on Hardy-Weinberg expectations by the use of Chi-square analysis (Steel & Torrie, 1960). Significance was determined at the 0.05 level of probability.

RESULTS AND DISCUSSION

Variation in bisexual populations

Of the 20 cistrons studied, eight (CAT, GPI, EST-1,2,3,4, PGM-2 and 6-PGDH) were polymorphic; the remainder of the cistrons surveyed were monomorphic for the same electromorph in all individuals surveyed. Genotypes, instead of electromorph frequencies, of individuals are given in Table 1 because they are the critical data. Two polymorphisms are of particular interest because they indicate regional geographic differentiation.

Four electromorphs were resolved for EST-2; the EST-2^b electromorph occurs at fixed or nearly fixed frequencies in populations east of the Apalachicola drainage system (Fig. 1: sites 6,7). This electromorph is in low frequency (sites 1,2) or absent (sites 3,5) in populations in the Apalachicola drainage system; it apparently is replaced in the latter by the

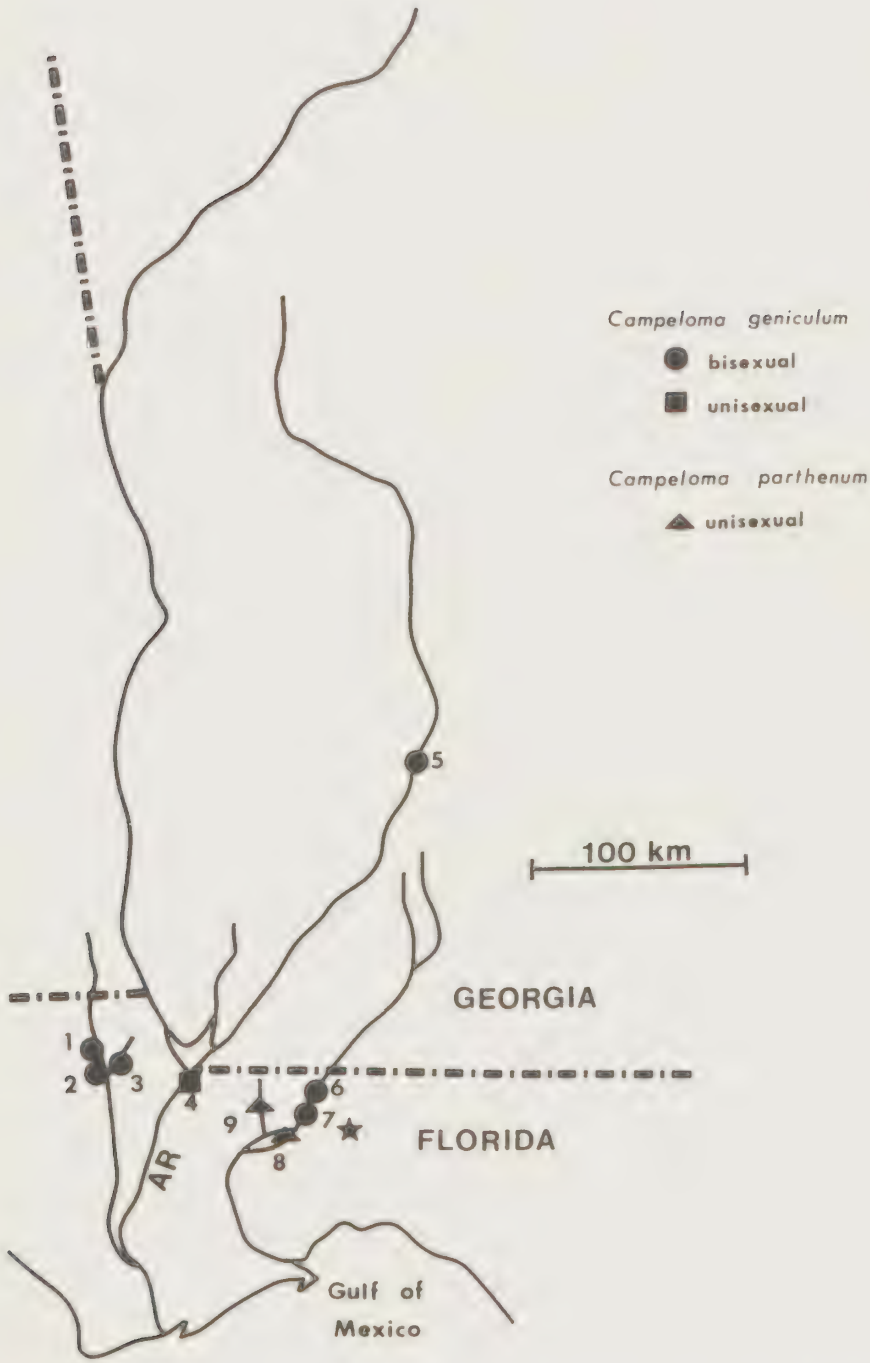

FIG. 1. Collecting sites of bisexual (1-3 and 5-7) and parthenogenetic (4, 8 and 9) *Campeloma*. Sites 1, 2, Chipola River; 3, Spring Creek; 4, North Mosquito Creek; 5, Flint River; 6, 7, Ochlockonee River; 8, Lake Talquin Reservoir; 9, Little River. AR = Apalachicola River; ★ = Tallahassee. (See Materials Examined section for more details on localities.)

TABLE 1. Genotypes of *Campeloma geniculum* from six bisexual populations.

Sample size	Enzyme							
	CAT	GPI	EST-1	EST-2	EST-3	EST-4	6-PGDH	PGM-2
				Chipola River/site 1				
males:								
4	b/b	b/b	b/b	c/d*	b/b	b/b	b/b	b/b
2	b/b	b/b	b/b	c/c	a/b	b/b	b/b	b/b
1	b/b	b/b	b/b	c/c	b/b	b/b	b/b	b/b
1	b/b	b/b	b/b	c/d	a/a	b/b	b/b	b/b
1	b/b	b/b	b/b	c/d	a/b	b/b	b/b	b/b
1	b/b	b/b	b/b	b/d	b/b	b/b	b/b	b/b
females:								
4	b/b	b/b	b/b	c/c	b/b	b/b	b/b	b/b
2	b/b	a/b	b/b	c/d	b/b	b/b	b/b	b/b
1	b/b	b/b	b/b	b/c	a/b	b/b	b/b	b/b
1	b/b	b/b	b/b	c/d	a/b	b/b	b/b	b/b
1	b/b	b/b	b/b	d/d	a/b	b/b	b/b	b/b
1	b/b	b/b	b/b	c/d	b/b	b/b	b/b	b/b
				Chipola River/site 2				
males:								
1	a/a	b/b	b/b	c/c	b/b	b/b	b/b	b/b
1	a/b	b/b	b/b	c/c	b/b	b/b	b/b	b/b
females:								
4	b/b	b/b	b/b	c/c	b/b	b/b	b/b	b/b
2	a/a	b/b	b/b	c/c	b/b	b/b	b/b	b/b
1	b/b	b/b	b/b	b/c	b/b	b/b	b/b	b/b
2	b/b	b/b	b/b	c/c	b/b	a/b	b/b	b/b
				Spring Creek/site 3				
males:								
6	b/b	b/b	b/b	c/c	b/b	b/b	b/b	b/b
3	b/b	b/b	b/b	a/c	b/b	b/b	b/b	b/b
1	b/b	b/b	b/b	c/c	b/b	b/b	b/b	a/b
females:								
5	b/b	b/b	b/b	c/c	b/b	b/b	b/b	b/b
4	b/b	b/b	b/b	a/c	b/b	b/b	b/b	b/b
1	b/b	b/b	b/b	a/a	b/b	b/b	b/b	b/b

TABLE 1. (Continued)

Sample size	Enzyme							
	CAT	GPI	EST-1	EST-2	EST-3	EST-4	6-PGDH	PGM-2
	Flint River/site 5							
males:								
1	b/b	b/b	b/b	c/c	b/c	b/b	b/b	b/b
1	b/b	b/b	b/b	c/c	b/b	b/b	b/b	a/b
1	a/b	b/b	a/a	c/c	b/c	b/b	b/b	a/b
1	b/b	b/b	a/a	c/c	b/b	b/b	b/b	a/b
1	b/b	b/b	b/b	c/c	b/c	b/b	b/b	b/b
1	b/b	b/b	b/b	c/c	b/b	b/b	b/b	b/b
females:								
3	b/b	b/b	a/a	c/c	b/b	b/b	b/b	b/b
2	b/b	b/b	b/b	c/c	b/b	b/b	b/b	b/b
2	b/b	b/b	a/b	c/c	b/c	b/b	b/b	b/b
2	b/b	b/b	b/b	c/c	b/c	b/b	b/b	b/b
1	b/b	b/b	a/a	c/c	b/c	b/b	b/b	a/b
1	b/b	b/b	b/b	c/c	c/c	b/b	b/b	b/b
1	b/b	b/b	a/a	c/c	c/c	b/b	b/b	b/b
1	b/b	b/b	a/b	c/c	c/c	b/b	b/b	b/b
1	b/b	b/b	a/b	c/c	b/b	b/b	b/b	b/b
	Ochlockonee River/site 6							
males:								
1	b/b	b/b	b/b	b/c	b/b	b/b	a/a	b/b
9	b/b	b/b	b/b	b/b	b/b	b/b	a/a	b/b
females:								
2	a/b	b/b	b/b	b/b	b/b	b/b	a/a	b/b
8	b/b	b/b	b/b	b/b	b/b	b/b	a/a	b/b
	Ochlockonee River/site 7							
males:								
5	b/b	b/b	b/b	b/b	b/b	b/b	a/a	b/b
females:								
5	b/b	b/b	b/b	b/b	b/b	b/b	a/a	b/b

*Underscoring indicates heterozygote; letters denote electromorph migration (see text).

EST-2^c electromorph. Similarly, two electromorphs were resolved for 6-PGDH: the 6-$PGDH^a$ electromorph was fixed in the eastern populations, while the 6-$PGDH^b$ electromorph was fixed in the western drainage system populations (Table 1). Further investigation of populations in other rivers in these and adjacent drainages is necessary to evaluate the significance of this apparent regional differentiation.

Two additional aspects of these data are significant. First, when these bisexual populations are considered as a whole (i.e., electromorph frequencies are combined for males and females), the genotypic frequencies observed are in close agreement with those predicted on the basis of Hardy-Weinberg expectations (χ-square, not significant). This result is interpreted as an indication that these individuals constitute a randomly breeding, sexually reproducing population. Secondly, heterozygotes were observed among both males and females. This result is interpreted to indicate that both males and females possess diploid genomes. Furthermore, no cases were found in which more than two electromorphs were present in an individual for any particular locus, which finding is also indicative of diploid genomes. Hence, there is no indication that the bisexual populations reproduce by asexual or parasexual (parthenogenetic, hermaphroditic) modes.

Variation in unisexual enclaves

Three distinct genotypes were found in the unisexual enclaves; two at sites 8 and 9, and one at site 4. Seventeen of the 19 individuals from Lake Talquin (*Campeloma parthenum*) were heterozygous for the same electromorphs for $GPI^{a/b}$, EST-$1^{b/c}$, EST-$4^{a/b}$, $IDH^{a/b}$, 6-$PGDH^{a/b}$, α-$GPDH^{a/b}$ and G-6-$PDH^{a/b}$; the remaining two individuals were also heterozygous for EST-$2^{a/b}$. All individuals from site 4 were heterozygous for the same electromorphs for $GPI^{a/b}$, EST-$2^{b/c}$, $IDH^{a/b}$, 6-$PGDH^{a/b}$ and α-$GPDH^{a/b}$. Thus each female from these samples was heterozygous for five (site 4), seven (sites 8 and 9) or eight (site 8) of the cistrons surveyed. Furthermore, the site 4 and sites 8 and 9 clones can be differentiated by their respective genotypes for EST-1, EST-2, EST-4 and G-6-PDH, while the two clones from site 8 can be differentiated by their respective genotypes for EST-2.

Two factors lead us to suggest that these "populations" are the result of parasexual reproduction. First, additional collections made during the past 7 years (Vail, 1978, 1979, 1980), consisting of over 7,000 individuals from these localities, have failed to locate male or hermaphroditic *Campeloma*. However, female *Campeloma* have been abundant. Other investigations of additional sites within the same rivers and lakes have yielded similar results. Furthermore, it was unusual to find all individuals heterozygous for five, seven or eight cistrons in these "populations", especially, when compared to the low heterozygosity observed in the bisexual populations previously discussed. Not surprisingly, when the genotypic frequencies of the unisexual enclaves were compared to those predicted based on Hardy-Weinberg expectations, all were found to be significantly different (χ-square, $P > 0.05$) as a result of the absence of homozygous genotypes. This result strongly implies non-random reproduction or, as males are absent, it implies parthenogenetic reproduction.

Mother-offspring analysis

Because adult female *Campeloma* are ovoviviparous, genetic analysis of mothers and their offspring is possible. However, three factors complicate this analysis. First, the production of one year's brood occurs during several months, and the simultaneously incubating young represent varying stages of development. Likewise, "births" occur during several months' time (see Vail, 1978). As a result of this "conveyor belt" system of brood production, the number of young per brood varied monthly according to the stage of the brood production cycle, so that the entire brood (= female's reproductive effort) is usually not present at any one time. Thus, we were not able to examine all the zygotes produced by one female. Second, even fully developed but still incubating young are less than 4 mm in diameter, and

most of the incubating young are smaller. Thus, as only minute amounts of embryonic tissue were available for analysis, only GPI, EST, IDH, α-GPDH and 6-PGDH were surveyed. Finally, electrophoretically detectable variation among adults from bisexual populations was slight (Table 1), indicating a high probability that a homozygous female would mate with a male homozygous for the same electromorph. Offspring analysis from such a mating would consistently demonstrate the same homozygous genotype and thus yield no useful information concerning the inheritance pattern of electromorphs. Hence, to conserve materials and to maximize the information obtained from mother-offspring analyses in bisexual populations, only offspring from heterozygous females were analyzed.

Three different genotypic ratios would be expected in our mother-offspring analyses: (1) female (heterozygous) x male (homozygous); this mating should result in offspring with two genotypes, 1 (homozygous) : 1 (heterozygous); (2) female (heterozygous) x male (heterozygous); this mating should result in offspring with three genotypes, 1 (homozygous) : 2 (heterozygous) : 1 (homozygous); and (3) female (parthenogenetic, heterozygous); this reproductive episode should result in all offspring being either homozygous (if automictic parthenogenesis) or heterozygous (if apomictic parthenogenesis) "carbon copies" of the maternal genotype. Of course, results 1 and 2 are the predictions for a diallelic system, in a sexually reproducing diploid population. Hence, sexual reproduction could be inferred from the presence of multiple genotypes in a brood with those genotypes in close agreement to expected ratios, whereas parthenogenetic reproduction could be inferred by the presence of only one genotype (either all homozygous, although two homozygous genotypes for automixis, or all heterozygous for apomixis) in the brood.

It is obvious from Table 1 that no "bisexual" females from sites 6 and 7 were heterozygous for any of the requisite cistrons; thus no offspring were analyzed from these populations. Only six adult "bisexual" females from site 1 and four adult "bisexual" females from site 3 were heterozygous for any of the requisite cistrons and possessed broods of young large enough to analyze (these snails were collected during the peak of their reproductive cycle in late October). The bisexual females from sites 2 and 5 were obtained in May 1980; the embryos were too small (4-16 cell stage) to examine. The results of the mother-offspring analyses are given in Table 2.

Segregation of electromorphs was observed for six cistrons (marked by * in Table 2). Although significant departures from expected genotypic ratios were noted in all cases, we do not find this result surprising in light of the "conveyor belt" system of brood production. The critical result is that in six cases multiple genotypes were observed in offspring of heterozygous mothers; this result indicates segregation and hence sexual reproduction occurs in these populations.

The observation of segregation in bisexual populations is in sharp contrast to the results obtained from the mother-offspring analysis of broods from unisexual enclaves. Seven females from each of two enclaves (sites 4 and 9) contained offspring, all of which were analyzed. All 150 young from these females were heterozygous for GPI, the respective EST cistron (that of the mother), 6-PGDH, IDH and α-GPDH, i.e., they were fixed heterozygotes. No segregation was observed; all young were "carbon copies" of the maternal genotype. This result, in addition to the apparent absence of males and the uniformity of genotypes within localities, confirms the occurrence of parthenogenetic reproduction. Furthermore, the absence of male *Campeloma* of these (*C. geniculum* or *C. parthenum*) or any other species at these localities precludes gynogenetic parthenogenesis, and the heterozygous genotypes observed in offspring of heterozygous mothers strongly suggest that apomictic parthenogenesis occurs in these clones.

Finally, it appears that at least two clones occur sympatrically in the Lake Talquin-Little River system. To date, only one clone has been identified from the Mosquito Creek system. Investigations are currently in progress to determine whether additional clones occur in these

TABLE 2. Genotypes of mothers and offspring from two bisexual populations of *Campeloma geniculum*.

Maternal genotype		Offspring genotype
Chipola River/site 1		
1) GPI	b/b	17b/b
EST-2	b/c+	0b/b:0b/c:17c/c
EST-3	a/b	0a/a:17a/b:0b/b
2) GPI	b/b	19b/b
EST-2	c/d	0c/c:0c/d:19d/d
EST-3*	a/b	3a/a:13a/b:3b/b
3) GPI	b/b	19b/b
EST-2	d/d	19d/d
EST-3*	a/b	1a/a:17a/b:1b/b
4) GPI*	a/b	0a/a:12a/b:2b/b
EST-2*	c/d	1c/c:13c/d:0d/d
EST-3	b/b	14b/b
5) GPI	b/b	17b/b
EST-2	c/d	17c/d
EST-3	b/b	17b/b
6) GPI*	a/b	3a/a:6a/b:0b/b
EST-2	c/d	0c/c:9c/d:0d/d
EST-3	b/b	9b/b
Spring Creek/site 3		
1) EST-2	a/c	0a/a:0a/c:20c/c
2) EST-2	a/c	0a/a:0a/c:14c/c
3) EST-2*	a/c	0a/a:4a/c:22c/c
4) EST-2	a/c	0a/a:0a/c:4c/c

+ = Underscoring indicates maternal heterozygous genotype.

* = Indicates multiple genotypes observed in offspring.

systems, as well as to determine whether additional enclaves of parthenogenetic *Campeloma* occur within the distribution of *C. geniculum*.

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UTILIZATION OF SOLAR ENERGY IN ACHIEVING FAVORABLE RURAL ECOLOGY IN EGYPT BY THE YEAR 2000. MASS SNAIL-HOST ERADICATION BY SOLAR ENERGY[1]

Hassan H. Khalil

ABSTRACT

Black polyethylene sheets, floated on the surface of tertiary canals in rural areas of Egypt, were found to be an efficient and inexpensive material to induce a considerable rise in water temperature within a few hours of exposure to sunshine. The degree of temperature rise was not compatible with snail survival, and therefore it is suggested that this approach should be developed as an emergency measure to break the cycle of schistosomiasis, pending the completion of the on-going covered drainage system project. By this method, no foreign element is introduced into the delicate ecology of the land, while the quality of life of the villagers and the local workers can be significantly improved.

INTRODUCTION

A general survey of the literature on schistosomiasis and the disastrous effects of this scourge on 250 million individuals worldwide makes it imperative that a rapid, aggressive and interdisciplinary approach should be put into effect where this age-old disease is endemic. This approach should be directed to prevent a) children from getting this inevitable infection and b) teenagers and working farmers from having repeated infections in spite of medical therapy.

A study of the life cycles of the three types of schistosomes infecting humans (*Schistosoma haematobium, S. mansoni, S. japonicum*) shows that parasite transmission occurs mainly during the warm months of the year when canal and agricultural water temperatures range from 25-30°C. Transmission is interrupted during the short winter months of tropical and subtropical regions.

Schistosomiasis is the major endemic disease affecting millions of Egyptian rural inhabitants, greatly reducing their physical and mental capacity (Khalil, 1978; Khalil et al., 1978). About 250,000 villagers are infected with schistosomiasis every year during the warm months of the year, i.e., between 500-1000 are infected every day (Z.Y. Seddik, Tarek H. El-Badawy & Hassan H. Khalil, pers. observ.).

Substantial resources, human, physical and financial, have been expended during the last fifty years in the hope of achieving a favorable rural ecology, free from endemic disease and illiteracy, so that the rural community may enjoy a more hygenic way of living. In spite of these efforts, poor sanitary conditions are still widespread throughout these communities and will continue to be so if not corrected. After several decades of research on schistosomiasis, no further time should be lost in the search for ways and means to limit and eventually to eradicate this disease, which recently has shown an unprecedented rate of spread. This increase is due to the recent considerable rise in the rate of population growth, as well as to several recently introduced changes in the Egyptian rural ecology.

The present system of rural canal maintenance limits the responsibility of the government authorities to clear and maintain the muddy banks of the primary and secondary canals only, while the farmers themselves are supposed to clear the tertiary irrigation and drainage canals. However, the present small land owners fail to coordinate their efforts to clear the tiny canals

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inside their property of weeds; the weeds help water to stagnate and offer a source of attachment to snails, thereby permitting a formidable population of snails to flourish.

Although an on-going governmental project of closed drainage is expected to reduce the incidence and prevalence of schistosomiasis, it may take two to three decades to cover the drainage network in Egypt.

The objective of the present work is to find an inexpensive way to break the cycle of schistosomiasis that could be applicable to the chronically poor rural environments, where schistosomiasis has been affecting the communities for the last 5000 years and has shown a recent thrust in its incidence and prevalence.

The literature on the life cycle of schistosomes shows that the life span of schistosomal cercariae which infect man is very dependent on the temperature of their environment. With the exception of *Schistosoma japonicum*, schistosomal cercariae are shed in tens of thousands from each infected snail during the warm seasons of the year. The cercariae hardly develop in the cold winter months. Unless they reach their definitive host (man), they survive only for 30-54 hrs in stagnant field canal water having a mean day temperature of 28°C. However, they have a shorter life at higher temperature and die within three minutes at 50°C and one minute at 55°C (Jones & Brady, 1947).

Although sunshine is favorable for the development of the snails and the cercariae which they shed, this same factor could be utilized to limit their survival and prevent the spread of this endemic disease, as well as other water-borne disease.

The snail hosts of *Schistosoma haematobium* (*Bulinus truncatus*) and of *S. mansoni* (*Biomphalaria glabrata*) are even more sensitive to temperature fluctuations than the cercariae which they shed. This fact has been known for years (Barlow, 1939; Standen, 1952; Stirewalt, 1954; Malek, 1958; Michelson, 1961; Shiff, 1964; Sturrock, 1966; Chernin, 1967; Berrie, 1969; Jobin, 1970). However, a recent experimental study showed that, when water temperature is maintained at 30°C, the gonads of these snails as well as other pulmonate snails do not develop and hence the snails do not lay eggs (van der Schalie & Berry, 1973). A more recent study to determine the tolerance of snail embryos to thermal stress showed that water temperatures above 35°C are lethal to these snails and their embryos (Siefker et al., 1977). On these grounds, the potential use of solar energy for snail-host control at focal points of farmers' gathering has been advocated; water circulated through standard solarators would be heated to temperature levels that stop the gonad development of snails, thus preventing egg laying, and that also kill the adult snails (van der Schalie & Blankespoor, 1977).

Although the authors of the last report show an accurate account of snail behaviour and chances of survival at different temperature levels, the method they advocate does not seem to be practical. It is not possible, at the present state of farmers' illiteracy and lack of adequate quantities of potable water supply, to stop or even reduce their daily exposure to widespread areas of polluted local canal waters which they need for their domestic functions and which also offer the only entertainment for their children during the summer months when infection reaches its peak (Fig. 1). Therefore, the potential use of solar energy at focal points in snail-host control cannot be a practical approach unless applied to large-scale projects of total snail eradication.

During the spring, summer and fall in tropical and subtropical regions, the daily land temperature reaches higher levels than that required to kill the intermediate hosts of schistosomiasis. However, river and canal waters of this same environment do not follow these land temperature levels and remain at lower levels, favorable for snail ecology. This discrepancy between land and water temperatures, which is well known to meteorologists and is partly responsible for weather changes, is due to two facts:

1) the specific heat of water is the highest of all known compounds; therefore, more calories are needed to raise the temperature of the canal water one degree centigrade than that of the surrounding earth;

FIG. 1. Summer activity in a rural Egyptian canal.

2) water vapor pressure increases with rising temperature, allowing more water to evaporate. Since every gram of water between 20° and 50°C takes 574 calories with it during the process of evaporation (Hodgman, 1961-62), in tropical and subtropical environments this vaporization heat loss maintains the mean canal water temperature below 30°C, while land temperature reaches much higher levels.

This study is an application of the above-mentioned facts of schistosomiasis control: *any method that prevents water evaporation by the abundant solar energy in the regions affected should, under the proper conditions, induce a substantial rise in the water temperature of the network of small irrigation and drainage canals to levels incompatible with snail survival.* However, the cost of applying this method over thousands of villages should be inexpensive, so that it lies within the economic ability of the countries concerned.

MATERIALS AND METHODS

Experimental simulation of a tertiary rural canal

Since the depth of water in the tertiary irrigation and drainage canals ranges between 30 and 50 cm, an experimental simulation of a small stagnant water canal was made. Glass 10 mm thick was cut and fastened with silicone rubber to make a rectangular container measuring 127 cm long, 26 cm wide and 39 cm deep. Two smaller water tanks made of the same materials were used as controls. The side walls were insulated from exposure to sunshine by multiple layers of newspaper and the bottom from ground heat by polystyrene foam. The containers were filled with raw canal water and about 500 schistosome host snails (*Biomphalaria boissyi* and *Bulinus truncatus*), with a few lettuce leaves to feed them, were placed in the tank inside a plastic sieve.

Solar heating of the water was started early in the day by placing a black polyethylene sheet 0.3 mm thick on the surface of the water in the large water tank, transparent polyethylene on the surface of one of the small control tanks, while the third was left uncovered. The three containers were placed in the sun on the roof of the research unit in Alexandria. Hourly measurements of water and ambient temperatures were recorded by mercury thermometers from 0800 until 1500 hrs over a period of several days in late August and early September 1979.

Field studies

After two weeks of cool and stormy weather, a few preliminary field studies were carried out in late September and early October 1979. A small drainage canal, 120 m long, 1.2 m wide and 60 cm deep, located 70 km southeast of Alexandria at Gianaclis farm, was used. Canal water, which was kept stagnant during the experiment, was covered by a long sheet of the same black polyethylene used in the simulation study. In order to keep the polyethylene sheets floating on the water and without large air pockets, several sticks of locally obtained reeds were spread out on the water to prevent the polyethylene from sagging under the water. This sheet was further anchored by similar reeds to the side banks of the canal to keep it stretched on the surface of the water. Hourly temperature measures were obtained of the water from the covered canal and from a similar uncovered one from 0800 until 1500 hrs on several warm days with clear skies, after a morning fog lasting until 0930-1000 hrs.

RESULTS

Experimental simulation of a tertiary rural canal

The experimental study in the three water tanks showed the following results (Fig. 2):

1) water temperature rise induced by solar heating through a black polyethylene sheet reached a peak of 47°C at 1500 hrs on the second day of exposure, 20°C higher than the starting morning temperature of the same day. The water in the tank covered with the same transparent material did not rise beyond 38°C. This difference is due to the fact that the black material, besides preventing water evaporation, is better able to absorb solar heat before transferring it by conduction to the underlying water;

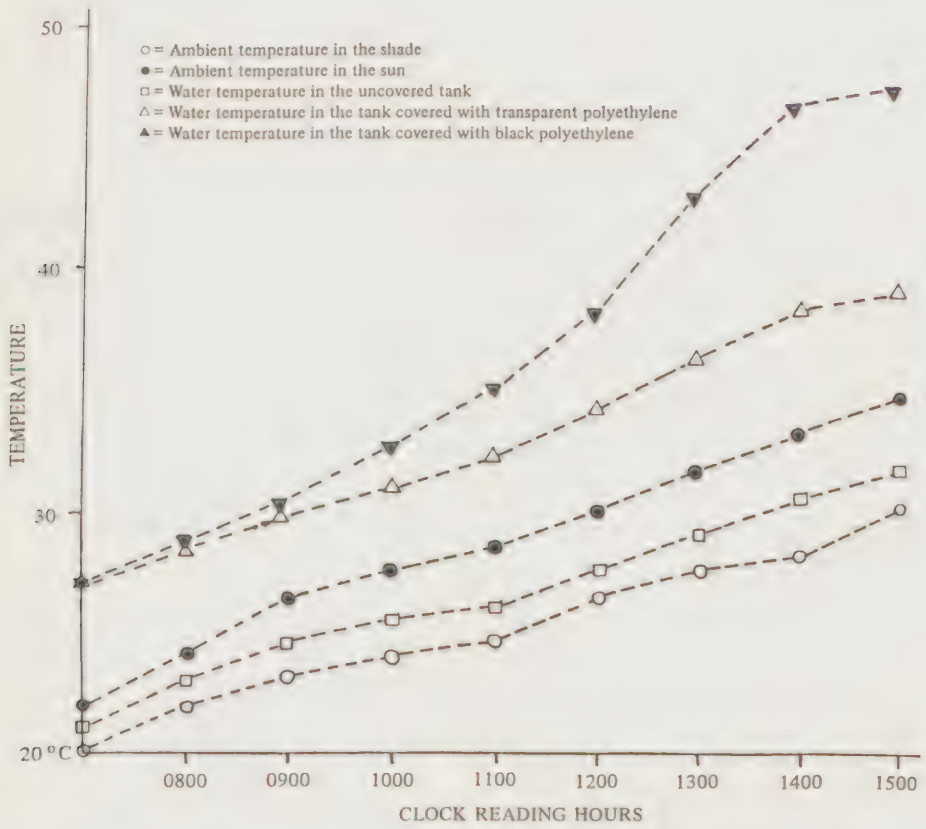

FIG. 2. Temperature measures during morning and afternoon hours on the second day of exposure.

2) water temperature rise in the uncovered tank remained within the range between the ambient temperature in the shade and that in the sun and did not rise beyond 31°C at 1500 hrs on the second day;

3) about one-third of the heat gained during the first day was retained overnight in both the black and transparent polyethylene-covered tanks, since the initial morning water temperature in both of these tanks was 7°C higher than that in the uncovered control tank. This observation shows that, within this temperature range, water covered by thin black or transparent polyethylene retains about one-third of the heat gained during the previous day;

4) the snails which were placed inside a plastic sieve were brought out and inspected when the water temperature reached 35° and 41°C. At 35°C the snails seemed to be hyperactive and partially out of their shells. When the snails were re-examined at 41°C, they were all dead. The same experiment was repeated several times with the same results.

Field studies

These preliminary studies were carried out in late September and early October 1979, with an ambient temperature in the shade ranging from 24°C at 0800 hrs to 32°C at 1500 hrs; the corresponding temperatures in the sun were 26° and 37°C. Water temperature measures which were obtained at 1500 hrs on two successive days from the surface of the covered canal were 10°C higher than those obtained from the uncovered one (Fig. 3). In the covered canal, a temperature gradient of 1-1.5°C was recorded between the bottom (50 cm) and the surface of the water.

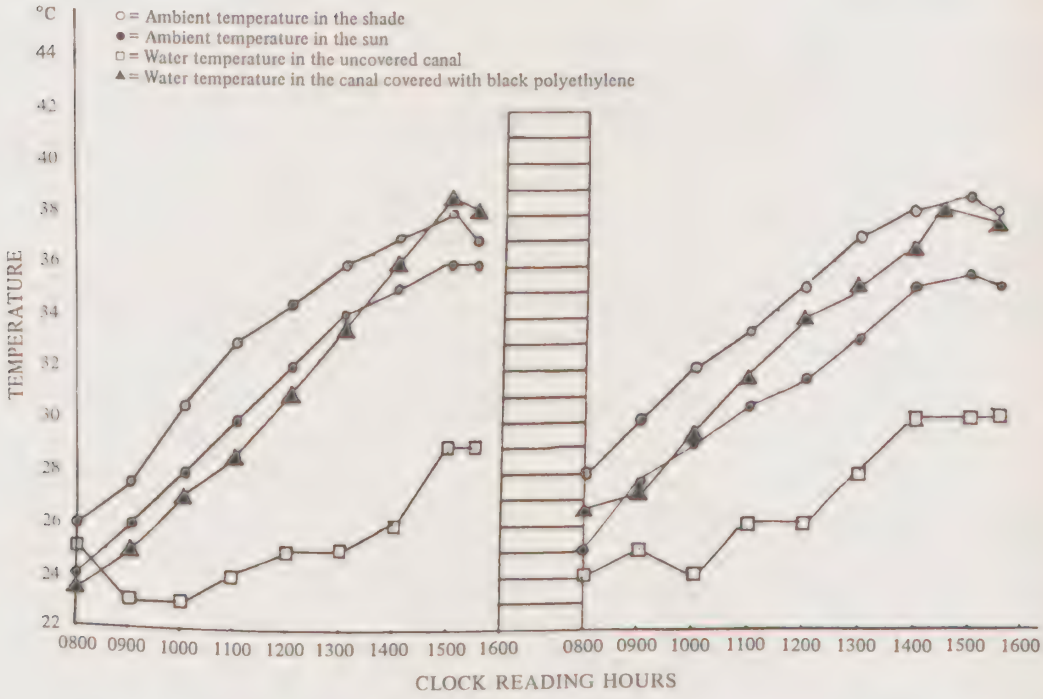

FIG. 3. Water and ambient temperature measures in the field studies in late September 1979.

DISCUSSION AND CONCLUSIONS

The high sensitivity of snail survival to temperature fluctuations has limited the spread of schistosomiasis to tropical and subtropical regions with poor sanitary conditions. During the short winter months of these regions, the incidence of schistosomiasis is limited by the cold weather because of a) limited exposure of the rural inhabitants to cold water and b) a large percentage of the snails apparently "hibernate" under the mud and therefore any hatching miracidia cannot reach them.

While cold weather limits the incidence of schistosomiasis and interrupts the life cycle of the parasite, the present approach is to use solar energy to raise the water temperature of drainage canals to levels that are incompatible with snail survival.

Transparent and black polyethylene sheets are very inexpensive materials and can be used several times and at different locations. However, black polyethylene is more effective since, besides preventing evaporation, it absorbs solar heat and transfers it to the underlying water better than the transparent material.

The field studies reported here were carried out in the fall with a relatively cool ambient temperature. A greater and more effective temperature rise is expected during the long and hot summer days of May, June and July, when even in the cooler Nile Delta the ambient temperature in the shade periodically exceeds 40°C. In the light of the earlier simulation studies, such conditions should be more than sufficient for reaching temperature levels lethal to the intermediate host, as well as other pulmonate snails.

To obtain maximal reduction of the snail population: a) primary treatment of these tertiary canals to remove weeds from their sloping muddy walls is essential before applying the proposed solar treatment; b) future canals should be planned away from the shade of trees and their banks also should be modified so that they can get maximal exposure to sunshine;

c) long distances of local canals should be covered during one or more successive hot summer days, as predicted by regional weather forecast; d) solar treatment should be applied on a large scale, covering the canals of one whole governorate at a time; e) the application preferably should be started upstream in Upper Egypt and moved in successive stages downstream to the Nile Delta and the governorates adjacent to the Mediterranean during the same summer.

This inexpensive water treatment by solar energy may have to be repeated every year or every few years to eradicate new snail colonies moving downstream from the large snail and infected baboon reservoirs at the origins of the Nile, mainly in Kenya and Uganda.

Besides the effect of ambient temperature, the extent of temperature rise by solar heating using this approach is inversely proportional to the depth of the treated canal and the velocity of water flow. To compensate for the water flow, long distances of the local canals should be treated at the same time. This application may not be practical for the Nile itself or primary canals, where the depth and velocity of the water may hamper its efficiency. This point should not be taken against the validity of this approach, since the main bulk of snail populations live and lay their eggs in the stagnant and shallow waters of the tertiary canals.

The present data suggest that, after almost complete eradication of the planorbids from the secondary and tertiary canals in Upper and Lower Egypt, an extension of this solar approach may be considered. More sophisticated and relatively more expensive methods (e.g., computer controlled plastic reflectors in conjunction with the black plastic cover) could be used to establish a permanent "snail barrier" over a suitable distance of the Upper Nile, to prevent living snails and their eggs from reaching downstream irrigation or drainage canals of the Nile Valley.

A single layer of black polyethylene was used in the present work because it is an inexpensive material. However, other variants of transparent plastic sheets made of polypropylene or any other suitable plastic should be manufactured and tried. Two layers of such material, with an upper transparent and a lower black one and with multiple vesicles of air between the two layers to keep the material floating with ease, should be more efficient than the single layer used in the present study. The suggested material would function as a very thin floating flat-plate collector, storing solar energy in the form of heat by a) preventing evaporation and b) transferring it to the underlying canal water.

The present study proves that solar energy can be used as a potent molluscicide, breaking the age-old life cycle of the parasite causing this formidable disease, without adding any chemicals or by-products and without introducing any harmful change into the ecology of the regions affected.

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SAMOANA JACKIEBURCHI, NEW SPECIES (GASTROPODA: PULMONATA: PARTULIDAE)

Yoshio Kondo

ABSTRACT

The new sinistral species of *Samoana* from Tahiti is dedicated to John "Jackie" B. Burch, Jr., with the name *jackieburchi*. This species is unique in having a sinistral shell shaped and colored exactly like its Tahitian co-inhabitant, *Partula otaheitana rubescens*. Its simple phallic interior of plain vertical ridges in contrast to *S. burchi*'s pendant pilaster nominates it as an ancestor to *S. burchi*.

Partulidae of Raivavae is amended to include *Partula hyalina*.

Samoana jackieburchi, new species (Figs. 1A to 1G, 2A to 2F)

Shell (Fig. 1A) sinistral, so closely resembling the sinistral shell of *Partula otaheitana rubescens* Reeve (Fig. 1I) in shell morphology and coloration that it is impossible to differentiate between them conchologically, and they are only differentiable by genital anatomy; subperforate, conic-turrite, solid, body whorl lemon-corneous, spire reddish, tip reddest. Aperture oblong-ovate, peristome reflexed into a solid lip, columella simple. Whorls 5½, flat on spire, convex on body whorl, crisscrossed by finely spaced microscopic spiral lines crossing over microscopic growth striae, each spiral stria peaking into a microscopic wavelet as it crosses over a vertical stria. Holotype Bernice P. Bishop Museum (BPBM) 9007 ex 1970-131.4(6); length 20 mm, diameter 11 mm, Faone Valley, Burch and Company (John B. Burch, Sr., James N. Cather, John B. "Jackie" Burch, Jr., Evin Oshima).

Genitalia (Fig. 2A). Hermaphrodite gland about 8-lobate, tightly compacted; hermaphrodite duct convoluted, well packed with contents at vesicula seminalis end. Albumin gland large; prostate also large. Uterus containing three embryos: first is free of eggshell, snail shell light brown; second and third embryos in cracking eggshells; the remaining oviduct a narrow tube; spermatheca short, elongate-cylindrical, twice the diameter of the oviduct, branching off high on the oviduct; vagina therefore long. Phallus (p) (Fig. 2B) small, short, ¼ oviducal length, C-shaped, curved-cylindrical; epiphallus (epi) off curved endpoint of phallus, thin, translucent, narrow, tubular, forming a loop above phallus, connecting with middle and apex of loop with main penial retractor (rp), this main retractor giving off a thin vestigial retractor (vrp) which is adhescent to the ascending half of the epiphallus-vas deferens loop and descends to the curving endpoint of the subphallus (p) to connect with it there.

Interior of phallus (Fig. 2C) cut vertically up the lesser curvature, has a series of four main vertical fleshy main ridges which give off smaller Y-shaped spurs or branches, which may occasionally anastomose with their neighbors.

Remarks. A comparable interior of a phallus from Aiavaro, collected by L.H. McDaniels in 1927, is offered here for comparison (Fig. 2D). The Aiavaro phallic specimen of *Samoana jackieburchi*, cut vertically up the greater curvature, reveals the simple architectural plan of vertical fleshy ridges, divisible into uprights and diagonals, without any special ornamentation accompanying these ridges.

The phallic interior of *Samoana jackieburchi* differs from that of the phallus of *S. burchi* Kondo (Kondo, 1973, p. 23, fig. 3C) in that *S. burchi* has a pendant pilaster hinged by a

lateral edge, whereas there is no such lingulate, spoon-shaped pilaster in *S. jackieburchi*, having only simple vertical fleshy ridges.

Subadult genitalia (Fig. 2E) immature: hermaphrodite gland 8-10 lobate, follicles immature, slim; hermaphrodite duct immature, convolutions just commencing. Albumin gland flat, unformed; prostate small, also unformed, ridged, backed by unformed preuterine oviduct. Uterus elongate, empty, pleated above, smooth below; spermatheca short, small; vagina medium. Phallus small (Fig. 2E,F), wound tightly into a C-shaped hook, its epiphallus plus vas deferens complex looped tightly with each other, requiring loosening (Fig. 2F) to reveal a narrow, translucent epiphallus (epi) and a narrower vas deferens (vd) connecting at retractor (rp), which provides a vestigial retractor (vrp) adhescent to the epiphallus to descend to the conical head of the subphallus (p); retractor thin, long.

Society Islands, Tahiti, Faone Valley, 1970-131.4, holotype BPBM 9007 ex 1970-131.4 (No. 6), 40 M, *Partula* on ginger, coffee, hibiscus, collected 29 June 1970 by Burch and Company.

Adult genitalia ex 1970-131.4(9) from an animal preserved whole with its shell, not from 9007 which had been separated from its shell in 1970. Subadult genitalia from animal preserved whole ex 1970-131.4(10).

Paratypes are from Faone, Mt. Aorai, Tiarei, Tautira, Faatautia, and Aiavaro.

Genitalia of *Partula otaheitana rubescens* (Fig. 2G)

A specimen of genitalia from Vaita, a shell of which is figured (Fig. 11), is illustrated here to show how different the genitalia of *Partula otaheitana rubescens* is compared with *Samoana jackieburchi*, even if their shells are like each other.

Albumin gland very small, almost depleted; prostate large, extensive. Uterus with two embryos, the older cleared to evacuate, the younger still within cracking eggshell; spermatheca more than ½ oviducal length, almost twice as broad as oviduct below older embryo at oviducal-spermathecal junction, split-off from oviduct high; vagina, therefore, long. Phallus very large, very long, about ¾ oviducal length, clavate, its epiphallus broader than subphallus; vas deferens inserting into epiphallus at its base or ½ way up the phallus; retractor thick, strongly contracted, short, and having an overhanging piece descending to mid-epiphallus, thence ending very near to vas deferens' connection to epiphallus.

Comparison in shells of *Samoana jackieburchi* and *S. burchi*

The differences between the shell of *Samoana jackieburchi* and that of *S. burchi* are as follows: *S. jackieburchi* is sinistral, larger, longer, sharper than *S. burchi*; whereas *S. burchi* is short and plump. In coloration, *jackieburchi* is lemon-corneous below, reddish above; whereas *burchi* is dark brown. In internal phallic structure, *jackieburchi* has plain vertical fleshy ridges; whereas *burchi* has a lingulate spoon-shaped pilaster pendant on one lateral side. Dimensional differences are: *jackieburchi* holotype is 20 x 11 mm, whorls 5½; *burchi* holotype is 16 x 9 mm, whorls 5⅓.

The 10 adult Faone Valley specimens (holotype plus nine paratypes, 1970-131.4) measure as follows: 17 x 10 mm (2), 18 x 10 mm (2), 19 x 10 mm (3), 20 x 10 mm (2), 20 x 11 mm (1) holotype; arithmetical average is 18.7 x 10.1 mm. Parenthesized numbers give the frequency.

Measurements of random selections of single shells in other paratype lots are: 37018 Mt. Aorai, 19 x 11 mm; 86756 Aiavaro, 19 x 10 mm; 1970-189(1) Tiarei, 18 x 10 mm; 1970-190B Tiarei, 15 x 10 mm; 1970-214(5) Faatautia, 17 x 10 mm; 1970-133.3(6) Faone, 19 x 10 mm; 1970-143(1 only) Tautira, 17 x 10 mm.

Paratypes from all locations (143 adult specimens complete with their animals, 129 already extracted out of the shells, 14 still entire (inside their shells, in alcohol)) are listed below.

L.H. McDaniels' 86690-86698 (31), 86700-86703 (8), 86745-86751 (22), Aiavaro; 86881 (3), Tautira. McDaniels collected in 1927 especially for Dr. C. Montague Cooke, Jr., while researching fei banana on Tahiti for the Bernice P. Bishop Museum.

Mangarevan Expedition of 1934 (led by Dr. Cooke) 137018 (9), 137019 (9), collected by Elwood C. Zimmerman, Donald Anderson, Yoshio Kondo, north slope of Mt. Aorai.

Burch and Company, 1970: Tiarei 1970-189 (24 plus 8 entire); Tiarei 1970-190B (1); Faatautia 1970-214 (9 plus 4 entire); Faone 1970-131.4 (8 plus 2 entire); Faone 1970-133.3 (4); Tautira 1970-143 (1).

Parenthesized numbers give the totality of specimens.

Brief descriptions of color photographed shells

Figures 1A to 1G are *Samoana jackieburchi*. Figures 1H and 1I are *Partula otaheitana rubescens.*

Samoana jackieburchi are:

1A. Faone 9007 ex 1970-131.4 (6): body whorl lemon-corneous, spire reddish, tip reddest.

1B. Faone 131.4 (10), subadult, lip not fully formed, all reddish, tip reddest.

1C. Mt. Aorai 137018 (9), body whorl light brown-corneous, spire reddish, tip reddest.

1D. Tiarei 189 (1), all reddish, tip dark red.

1E. Faatautia 214 (5), body whorl lemon-corneous, spire reddish, tip reddest.

1F. Tautira 143 (1 only), all corneous, tip barely reddish.

1G. Aiavaro 86756 (5), almost all reddish, tip reddest.

Partula otaheitana rubescens are:

1H. Tiarei 186.2 (4), all reddish.

1I. Vaita 86820 (10), body whorl plus penultimate whorl brownish-corneous, spire and tip reddish.

Two color forms are all reddish and two-toned.

Parenthesized numbers give that shell's numerical place in that lot. For example, in Figure 1A, Faone 9007 ex 1970-131.4 (6) means shell No. 6 of 8 shells of 131.4.

This new form of *Samoana* is dedicated to the late son of Dr. and Mrs. John B. Burch, Sr., of the Museum of Zoology, The University of Michigan, Ann Arbor, who took part in the Tahitian, Moorean and Raiatean portion of the Bishop Museum's Partulidae Program in 1970.

It is appropriate that two new species of Tahitian *Samoana*, *burchi* Kondo 1973 and *jackieburchi* Kondo 1980, are dedicated to Jack Burch, the father, and Jackie Burch, the son, for without their field researches in Tahiti, the genital anatomy of the Tahitian Partulidae would not be known as of 1980.

Hypothesis of descent in *Samoana* of Tahiti re-examined

Samoana jackieburchi is nominated to be the descendant of the earliest *Samoana* reaching Tahiti (compare Kondo, 1973: 31), possibly senior to *S. burchi*, owing to its simple phallic interior (only fleshy ridges) in contrast to *S. burchi*'s more elaborate phallic interior (a lingulate, spoon-shaped pilaster). The possibility that *jackieburchi*'s phallus is secondarily simplified must be taken into account also, but not in the present hypothesis.

The large size of its shell, sinistrality, and lemon plus reddish coloration should not influence a snail taxonomist's thinking. In the coming anatomical monograph of Tahitian Partulidae, it will be shown that a parallel case in dextral and sinistral *Partula affinis* Pease exists in southern Tahiti Nui. The small ovate-conic dextral, dark brown *P. affinis* has evolved a very large sinistral form in this region. It will be shown that Crampton's map (1916, text fig. 7, p. 115) will need the addition of *affinis* to accompany *sinistrorsa-sinistralis* distribution there to the tune of *affinis* 72%, *sinistrorsa-sinistralis* 28%, by Burch and Company's collections in that region.

Whether the dextral form came first, giving birth to the sinistral form in *Partula affinis* and in *Samoana jackieburchi* (sinistral) versus *S. burchi* (dextral) are moot questions.

Attention is called to the following: *Partula otaheitana affinis* will be elevated to *Partula affinis*. Hyphenation of *sinistrorsa-sinistralis* means that these two forms are indistinguishable.

Raivavae and *Partula*

In the 1973 paper (p. 31, bottom), I made a bold statement as follows: " . . . that *Partula* moved eastward behind *Samoana* and colonized Society, too, but never reach[ed] Raivavae, Rapa and Marquesas . . . " Strike out *Raivavae*. In 1973, I depended on the opinions of Pilsbry (1909-1910, p. 181) and Crampton (1916, p. 54-56), which is a very poor excuse: that *Partula hyalina* Broderip, which inhabits Cook, Austral Islands (Raivavae, Tubuai, Rurutu, Rimatara) and Tahiti was possibly man-carried. Proof of non-carriage by man surfaced on Rurutu on September 9, 1978, when some eggshelled embryos were discovered in *P. hyalina*; whereas *P. hyalina* (and its hypothetical offshoot *P. clara*) of Tahiti regularly have nude (without eggshell) embryos.

We now have to go back to Pilsbry's second hypothesis (1909-1910, p. 181) that *Partula hyalina* belongs to an ancient stock which populated Cook, Austral, and Tahiti when these mountain tops were the sierras of a large land mass. Crampton appears to favor Pilsbry's land mass hypothesis.

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FIG. 1. **A**, Holotype of *Samoana jackieburchi*, Faone. **B**, Paratype of *S. jackieburchi*, Faone. **C**, Paratype of *S. jackieburchi*, Mt. Aorai. **D**, Paratype of *S. jackieburchi*, Tiarei. **E**, Paratype of *S. jackieburchi*, Faatautia. **F**, Paratype of *S. jackieburchi*, Tautira. **G**, Paratype of *S. jackieburchi*, Aiavaro. **H**, *Partula otaheitana rubescens*, Tiarei (cf. 1B,D). **I**, *P. o. rubescens*, Vaita (cf. 1A,E).

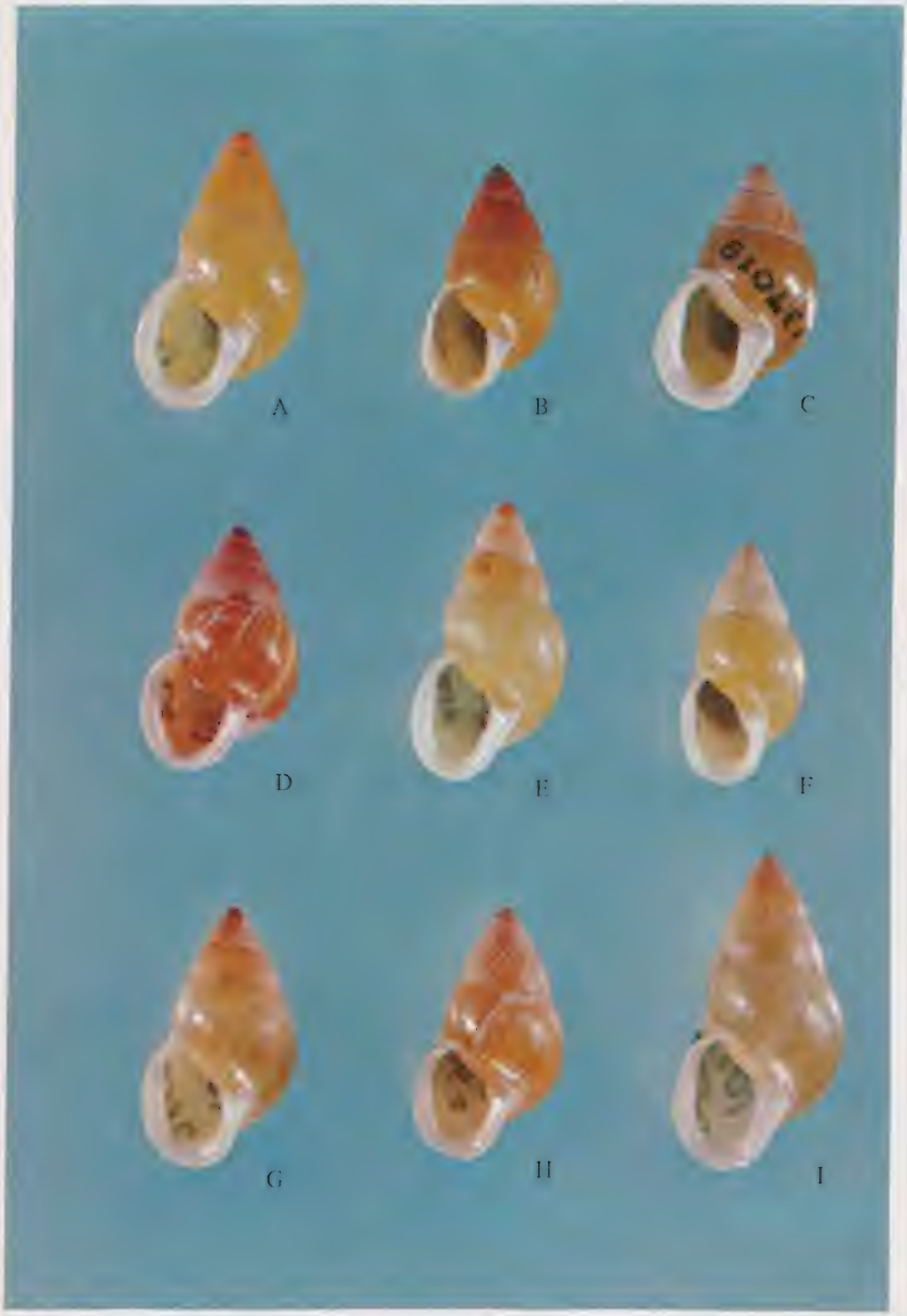
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FIG. 2. **A,** Genitalia of *Samoana jackieburchi*, Faone. **B,** Closeup, phallus of *S. jackieburchi*, external view. **C,** Internal topography of the phallus of *S. jackieburchi*. **D,** Phallus of *S. jackieburchi*, Aiavaro (cf. 2C). **E,** Subadult genitalia of *S. jackieburchi*, Faone. **F,** Closeup, subadult phallus of *S. jackieburchi*. **G,** Genitalia of *Partula otaheitana rubescens*, Vaita (cf. 2A).

Abbreviations: ag, albumin gland; epi, epiphallus; ovd, oviduct; p, phallus; pr, prostate; rp, retractor of phallus; sp, spermatheca; sub, subphallus; vag, vagina; vd, vas deferens; vrp, vestigial retractor of penis.

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FACTORS INFLUENCING GESTATION LENGTH IN TWO LAND SNAILS, *ACHATINA FULICA* AND *MACROCHLAMYS INDICA*

S.K. Raut and K.C. Ghose

ABSTRACT

Gestation length in land snails varies with the species. In nature, under favourable conditions the gestation period is 24.42 ± 5.2 days for *Achatina fulica* and 11.17 ± 1.8 days for *Macrochlamys indica*. Gestation was delayed in snails subjected to aestivation by altering their environment immediately after mating. A direct relationship exists between the length of aestivation and the gestation period. Aestivation for 15 days delayed egg laying by 1.35 and 5.61 days in *A. fulica* and *M. indica*, respectively. The delay was as long as 20.16 and 29.43 days in *A. fulica* and *M. indica*, respectively, after aestivating for 105 and 150 days, beyond which no brood was obtained.

INTRODUCTION

Gestation length plays an important role in population biology. Studies on extrinsic factors influencing gestation period are restricted mostly to the higher animals. Information on this point in molluscs is limited to *Achatina fulica* Bowdich (Kekauoha, 1966), *Helix aspersa* Müller (Herzberg & Herzberg, 1962) and *Limicolaria martensiana* Smith (Owiny, 1974). In an active state, particularly during the monsoon, the shortest gestation length in *A. fulica* is 20 days (Raut & Ghose, 1979). The maximum gestation length is not on record. Terrestrial snails aestivate for eight months in West Bengal (Ghose, 1959; Raut & Ghose, 1977), and information on the role of prolonged aestivation on the gestation length would be interesting. A series of experiments were conducted on those aspects on *A. fulica*, an introduced species, and on *Macrochlamys indica* Godwin-Austen, a native of Indian Union, and the findings are communicated here.

MATERIALS AND METHODS

To obtain specimens mating for the first time after the attainment of sexual maturity, *Achatina fulica* and *Macrochlamys indica* of 40 mm and 8 mm size, respectively, were isolated and kept active. The stage for isolation of the snails was based on the records of the size of the snails at which they laid their first batch of eggs. The size was 59 x 27 mm (Ghose, 1959) and 60 mm (Meer Mohr, 1949) for *A. fulica* and 12 x 8 mm (Ghose, 1959) for *M. indica*. In the present study, the first mating was recorded in control *A. fulica* and *M. indica* of 52 mm and 10.5 mm size, respectively. Isolated snails were kept in pairs at that age for first mating. Gestation length is designated as the time between mating and first egg laying and is considered as control below. The gestation length in the aestivation experiments is designated as the time from arousal from aestivation until laying of eggs. No snail was found to lay eggs during aestivation, which was always induced immediately following mating.

Gestation length – Control

Twenty and 10 pairs of active cage-reared snails of each of the species *Achatina fulica* and *Macrochlamys indica* were selected immediately after first mating since their attainment of sexual maturity between March 30 and April 3, 1975 and 1976, respectively. They were marked pairwise. For economy, one *Achatina* and one *Macrochlamys* were released in one cage measuring 200 x 200 x 250 cm, with fine wire netting on the sides and the top. The open lower end of the cage was placed on loose, moist soil, in a shady place on the Calcutta University campus, Ballygunge, Calcutta. The snails were kept active for a period of 75 days. In 1975, the snails were artificially activated, while in 1976 they became active without any such measures. Choice food-plants were supplied regularly.

Gestation length – Aestivation

Twenty-eight cages of the same specification as used in the previous experiments were kept in a place protected from the sun and rain. Eighty-seven and 88 pairs of *Achatina fulica* and *Macrochlamys indica*, respectively, were collected, in the first half of April 1976, from the cage-reared snails immediately after their first mating since attainment of sexual maturity. The mated pairs collected in a day were considered for one set of experiments. They were forced to aestivate on the next day in cages by controlling the environment. The snails were kept in aestivation for 15, 30, 45, 60, 75, 90, 105, 120, 135, 150, 165, 180, 195 and 210 days, i.e., successively increasing the period of aestivation by 15 days.

After the desired period, the snails were made active by spraying them with water and transferring them to cages, one snail in each cage. Here they were maintained for a period of 75 days for egg laying observations. They were kept under the most favourable conditions and supplied with adequate food.

RESULTS

Control

All of the 60 control *Achatina fulica*, a total of two years' experiments, laid their eggs 20 to 43 (24.42 ± 5.2) days after mating. Of the 40 snails observed in 1975, 12 individuals laid eggs on the 20th day after mating, 13 between 21 to 24 days, 10 between 26 to 29 days and the remaining 5 snails laid eggs between 32 to 41 days. On the other hand, of the 20 snails observed in 1976, 5 laid eggs on the 20th day, 5 between 21 to 26 days, 5 between 31 to 34 days and the remaining 5 deposited eggs between 38 to 43 days. It is calculated that out of a total of 60 snails, 17 (28.3%) laid eggs on the 20th day, 16 (26.6%) between 21 to 25 days, 12 (20%) between 26 to 29 days and the remaining 15 (25%) laid eggs between 31 to 43 days.

Out of the 60 *Macrochlamys indica* studied, 59 laid eggs between 10 to 17 (11.17 ± 1.8) days. Of the 40 snails observed in 1975, 19 laid eggs on the 10th day, 16 between 11 to 14 days and 4 laid eggs between 15 to 17 days. One snail failed to lay eggs. In 1976, out of 20 individuals, 9 laid eggs on the 10th day, 5 between 11 to 14 days and 6 between 15 to 17 days. Of the total 59 snails, 28 (47.45%) laid eggs on the 10th day, 21 (35.59%) between 11 to 14 days and 10 (16.94%) between 15 to 17 days.

Aestivation

The snails forced to aestivate for different periods had different gestation lengths. A direct relationship between the gestation period and the period of aestivation was recorded in both species (Table 1). *Achatina fulica*, undergoing aestivation for the shortest period, i.e., 15 days, laid eggs between 23 to 28 days, while the gestation period was 14 to 21 days in *Macrochlamys indica* aestivating for the same period. The permissible length for aestivation to enable *A. fulica* to produce a brood was 105 days, and the eggs were laid between 39 to 50 days after awakening. The period was longer for *M. indica*, i.e., 150 days, and the eggs were laid between 34 to 47 days after regaining activity.

DISCUSSION

The results of the experiments enable us to suggest that the minimum gestation length for *Achatina fulica* and *Macrochlamys indica* is 20 and 10 days, respectively, in their active season, in their natural habitat or in an environment simulating their natural environment. Egg laying was delayed up to 43 days in *A. fulica* and 17 days in *M. indica*, but the number of such cases was rather small.

A number of factors, e.g., ovulation, albumen production, reserve calcic substances and other physiological conditions of an individual, directly influence the production of a brood. It is most likely that lack of any one or more of these factors might have delayed the process of egg laying.

TABLE 1. Delay in egg laying in mated *Achatina fulica* and *Macrochlamys indica* due to aestivation.

Pairs taken		Length of aestivation (in days)	No. of individuals laying eggs		Period between awakening and egg laying (in days ± S.D.)	
A. fulica	*M. indica*		*A. fulica*	*M. indica*	*A. fulica*	*M. indica*
5	7	15	9	14	23-28 (25.77 ± 1.79)	14-21 (16.78 ± 2.23)
6	6	30	11	12	25-30 (27.18 ± 1.99)	14-27 (18.83 ± 4.63)
5	7	45	10	13	29-45 (34.70 ± 4.21)	19-28 (28.30 ± 3.62)
8	6	60	8	11	32-48 (37.75 ± 5.87)	23-32 (27.00 ± 2.73)
5	8	75	7	15	33-48 (41.14 ± 5.79)	23-38 (30.26 ± 5.15)
5	6	90	7	12	35-47 (43.28 ± 3.61)	26-41 (32.16 ± 4.54)
6	6	105	5	11	39-50 (44.60 ± 4.31)	27-39 (33.36 ± 4.35)
7	6	120	–	10	–	30-41 (36.20 ± 4.44)
6	5	135	–	7	–	32-44 (38.20 ± 3.36)
6	6	150	–	5	–	34-47 (40.60 ± 4.40)
7	7	165	–	–	–	–
9	6	180	–	–	–	–
6	6	195	–	–	–	–
6	6	210	–	–	–	–

As a rule, reserves are used up during aestivation to maintain a minimum metabolism. The longer the period of aestivation, the greater is the amount of reserves spent, and the longer will be the period required after activation to compensate for the loss and to resume normal activities.

The time required for resumption of reproductive activity in both species under investigation varied with the period of aestivation, which suggests that this function is equally subjected to the adverse effects of aestivation, though preparation for reproduction has been reported in aestivating *Achatina fulica* and *Macrochlamys indica* (Ghose, 1960).

The earliest brood in *Achatina* aestivating for 15 days was obtained on the average 25.77 days after awakening, i.e., it was delayed by 1.35 days longer than in the control. Aestivation for a period of 30, 45, 60, 75, 90 and 105 days delayed egg laying by 2.76, 10.28, 13.3, 16.72, 18.86 and 20.18 days, respectively. In *Macrochlamys indica*, the corresponding period was 16.78 and 5.61 days for the earliest brood after 15 days of aestivation. Egg laying required 7.66, 11.73, 15.83, 19.09, 29.99, 22.19, 25.03, 27.03 and 29.43 more days for snails aestivating for 30, 45, 60, 75, 90, 105, 120, 135 and 150 days, respectively.

It may be presumed that, though *Achatina* is acclimatized to Indian conditions for a little less than two centuries, their adaptation to tide over aestivation hazards is not at par with that of the *Macrochlamys*, a native snail, which is capable of retaining egg laying capacity for 45 days more, in spite of their much smaller size and consequently less stored materials. Interestingly, the delaying effect of aestivation on *A. fulica* was not significant until 45 days, while it was pronounced in *M. indica* at 15 days. It appears that the depletion of reserve materials in *A. fulica* is not great in snails aestivating for 30 days.

A long gestation period is always advantageous to a species in populating new areas, since adverse conditions in transport to other places by various agencies do not jeopardise their ability to produce offspring. Further, a single mated individual is capable of establishing a

species in a new place. The prolonged gestation periods in pestiferous snails should serve as a warning to governments to enforce strict quarantine measures.

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A NEW HELICARIONID LAND SNAIL FROM THE SOUTHEASTERN UNITED STATES

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ABSTRACT

Dryachloa dauca n. gen., n. sp. (Gastropoda: Pulmonata: Helicarionidae) is described from Florida and Alabama. It is most closely related to *Guppya* and *Euconulus*. The species lives deep in grass roots in wet and marshy habitats.

INTRODUCTION

The North American molluscan fauna has been intensively studied since the early nineteenth century and is one of the best known invertebrate faunas of the world. Nonetheless, a modest number of new taxa continue to be discovered, most notably from the austroriparian zone of the Southeast. Some of these discoveries occur in microhabitats that simply were overlooked previously. This paper deals with a species that inhabits one such microhabitat: the root-mass of grasses that grow in damp or marshy habitats.

MATERIALS AND METHODS

The anatomical material upon which the following data are based was collected by Harry G. Lee at the type locality during April-July, 1978. On all occasions specimens were sparse. They were kept alive in a glass jar on moist paper towels until July 16, 1978, at which time they were narcotized in an aqueous solution of chloral-hydrate, fixed in Bouin's fixative and preserved in 70% isopropanol. Gross anatomical dissections were made under a Wild M-5 dissecting microscope after specimens were lightly stained with Semichon's aceto-carmine stain. Isolated anatomical systems were stained with Harris' haematoxylin stain. Scanning electron micrographs of shells and radulae were made with a JEOL JSM-35C scanning microscope at the Department of Materials Science and Engineering, University of Florida.

Dryachloa new genus

Type species: *Dryachloa dauca*[1] new species

Shell minute, about 1.8-2.2 mm in major diameter; transparent, light amber colored; depressed-helicoid, with about four whorls; periphery rounded. Umbilicus narrow, perforation closed internally by a plug. Peristome simple, lunate; aperture without internal lamella or teeth. Embryonic whorls sculptured with very fine pits arranged in spiral rows. On later whorls spiral sculpture coalescing to form spiral striation that may become obsolete or absent on last whorl. Superimposed on this are relatively coarse thread-riblets. Caudal horn present, extending over caudal foss. Mantle collar with right and left shell lobes. Radula with tricuspid central; laterals tricuspid, bilaterally asymmetrical, in slightly oblique series; marginals bicuspid. Spermatheca small, clavate, on male side of vagina. Penis with large diverticulum. Penis sheath absent. Epiphallus simple, without caecum or flagellum. Prostate extending nearly full length of uterus.

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[1] Etymology: *Dryachloa* (f.) from the Classical Greek, *dryas*, a nymph, and *chloe*, a grass, connoting a nymph that lives in grasses; *dauca*, Gr., a carrot, in reference to the carrot-colored digestive gland in live animals.

Dryachloa dauca new species

Shell. Minute, depressed-helicoid (Fig. 3E-G), about 0.61-0.65 times as high as wide; transparent; grayish orange, shiny. Umbilicus narrow, almost occluded by peristome. Umbilical perforation closed by an internal plug. Whorls about 3.8-4.5; 1.0 embryonic whorls; suture moderately impressed, with a narrow hyaline zone, not descending at aperture. Whorls slightly arched between suture. Body whorl nearly uniformly rounded with periphery slightly above equator. Whorls sculptured with fine irregular axial growth wrinkles and spiral striations. Axial striations strongest dorsally (Fig. 1D), much weakened ventrally (Fig. 1G). Spiral sculpture very fine, faintly distinguishable with light microscopy, beginning on apical whorl as rows of punctate pits (Fig. 1F) which become more attenuated and fused on subsequent whorl (Fig. 1D,E); on last whorl spiral sculpture modified into continuous spiral striations (Fig. 1H,I), usually most distinct ventrally. Spiral sculpture highly variable; some shells nearly devoid, others densely sculptured. Aperture semilunate, lying at about 15° to shell axis. Peristome simple, sharp. Columella with a small tongue-like projection extending partially over umbilicus (Fig. 1G). Columella internally with a slight knob-like bulge.

Measurements in mm of seven individuals are given in Table 1.

TABLE 1. Measurements in mm of holotype (UF 22883) and six paratypes of *Dryachloa dauca*.

Specimen	Diameter			Aperture		
	Height	Major	Minor	Height	Width	Whorls
UF 22883	1.13	1.88	1.62	0.82	1.00	3.8
AMNH 189622	1.17	1.85	1.68	0.80	1.02	3.8
ANSP 350467	1.17	1.85	1.63	0.83	1.05	4.0
FMNH 198744	1.32	2.07	1.83	0.90	1.10	4.3
MCZ 288513	1.17	1.93	1.71	0.88	1.05	3.9
UMMZ 250063	1.37	2.17	1.98	0.98	1.24	4.3
NMNH 784629	1.29	2.00	1.85	0.90	1.12	4.1

UF = Florida State Museum; AMNH = American Museum of Natural History; ANSP = Philadelphia Academy of Natural Sciences; FMNH = Field Museum of Natural History; MCZ = Museum of Comparative Zoology; UMMZ = University of Michigan, Museum of Zoology; NMNH = National Museum of Natural History.

External anatomy. Sole narrow, long, about twice minor diameter of shell, tripartite. Caudal horn subterminal (Fig. 3B,C). Caudal foss a narrowly triangular vertical pore on posterior end of caudal horn (Fig. 3B). A narrow impressed mid-dorsal groove extending forward from caudal horn for half length of posterior foot. Mantle collar with two moderately long shell lobes (Fig. 3D) and three mantle lappets. Right shell lobe slightly longer than left shell lobe. Anterior left mantle lappet larger than other lappets; posterior left mantle lappet low, narrow; right mantle lappet with a tongue-like extension over pneumostome. Genital opening below and slightly anterior to right eye stalk. Eye stalks very slender, nearly equal to minor diameter of shell. In life extended soft parts slate gray, with sparse peppering of black more concentrated dorsally, especially on head and tentacles. Pallial tissue appearing apricot yellow through shell. Digestive gland lightly speckled with black. Hermaphroditic gland carrot red. Ocular retractor muscles black.

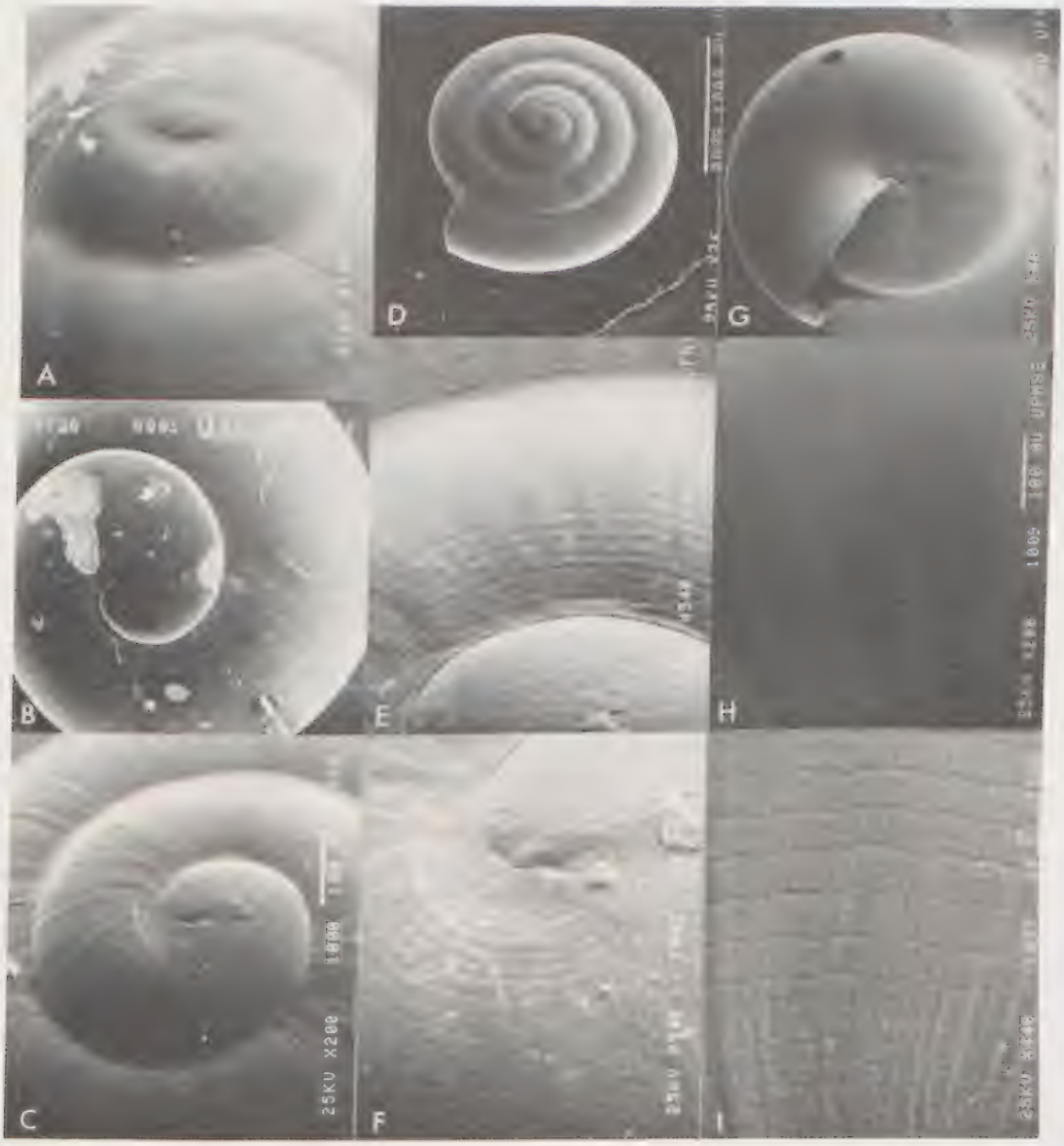

FIG. 1. Shell sculpture. A, *Guppya gundlachi* (Pfeiffer), Dominican Republic, Independencia Province, 4 km NE of El Aguacate, 810 m, UF 22889, X75. B, *Eucomulus chersinus chersinus* (Say), Florida, Alachua Co., Gainesville, UF 22890, X60. C, *Dryachloa dauca* n. sp., paratype, UF 22886, X100. D, *D. dauca*, paratype, UF 22885, X18. E-I, *D. dauca*, paratypes, UF 22886; E, X270; F, X270; G, X24; H, X100; I, X220.

Radula. Radular formula: $(C\frac{1}{3}\,L\frac{7}{3}\,M\frac{13}{2})$ 69-70 (two specimens examined). Central and laterals forming nearly straight transverse rows; marginals slightly oblique. Central narrower than adjacent laterals, tricuspid with elongate mesocone (Fig. 2A, B). Laterals tricuspid, asymmetrical, in slightly oblique transverse rows; mesocone elongate, endocone farther forward than ectocone (Fig. 2A, B); seventh lateral transitional to next marginal, endocone vestigial (Fig. 2B). Marginals bicuspid, with elongate mesocone and a subequal ectocone;

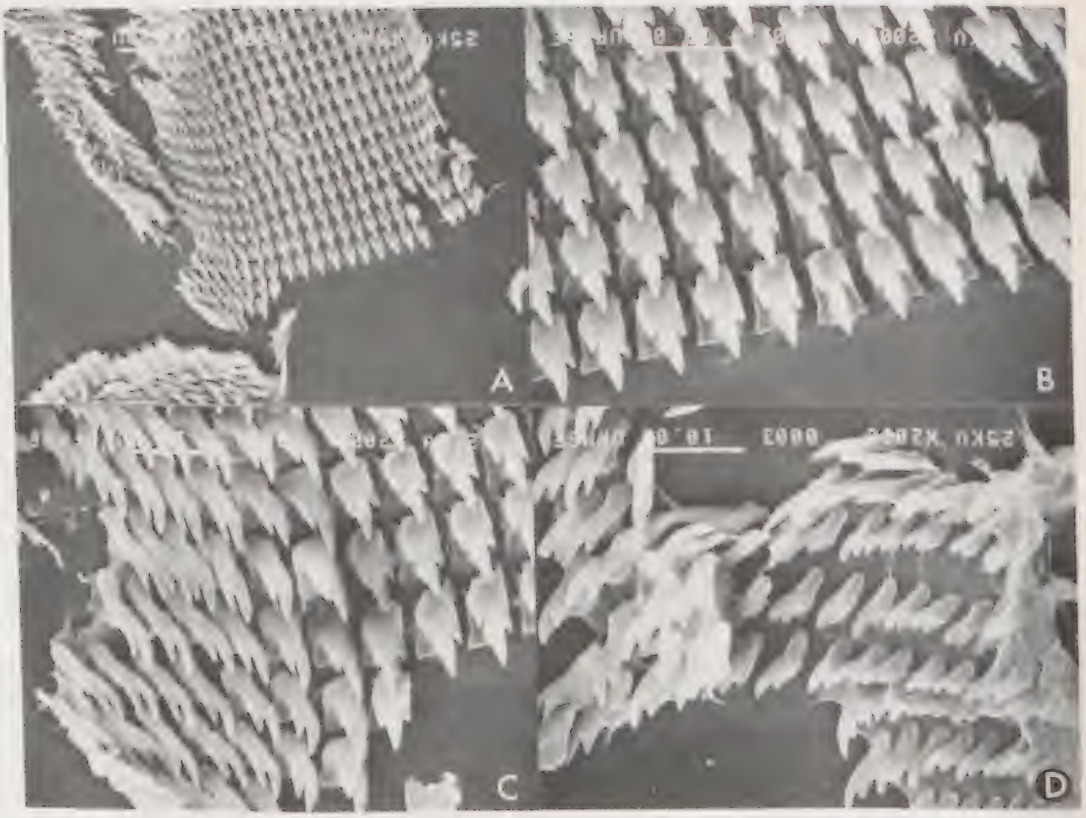

FIG. 2. Radula of *Dryachloa dauca* n. sp., topotype, UF 22887. A, X279; B-D, X1070.

marginals 1-7 with cusps extending mesad and forward over next tooth (Fig. 2C). Outermost marginals very reduced in size (Fig. 2D).

Reproductive system (Fig. 3A). Atrium opening immediately below and a little in front of right eye stalk. Right ocular retractor muscle passing between penis and vagina. Penial retractor muscle long, slender, inserting on apex of epiphallus, not enclosing vas deferens, originating on diaphragm beside albumen gland. Ovotestis (not illustrated) imbedded on dorso-columellar side of digestive gland, consisting of two clusters of 4-5 claviform lobes each; talon small, elliptical; carrefour not observed. Albumen gland large, irregularly ovate, consisting of large loosely cemented cells; with a shallow groove on ventral surface where gland overlays intestine. Uterus capacious along lower half. Species oviparous; no indication of uterinal embryos in specimens collected at different times of year. Vagina moderately capacious, almost twice as long as atrium, bearing a small clavate spermatheca at its base on male side of vagina just above junction with penis (illustration shows it on opposite side because of twisting when mounted on slide). Prostate nearly as long as uterus, consisting of relatively large convoluted lobes. Vas deferens slender, simple, without accessory glands or caeca, entering apex of epiphallus beside insertion of penial retractor muscle. Epiphallus small, bulbous, on apex of penis, without caecum or flagellum. Penis plus epiphallus slender, about twice length of vagina. Lumen of penis lined with low longitudinal folds of tissue. Penis with a large diverticulum near its base. Diverticulum tightly bound to penis with muscle sheet, longer and more voluminous than penis, but folded back upon itself so that it terminates at epiphallus. Lumen of diverticulum with large bulbous pilaster just above

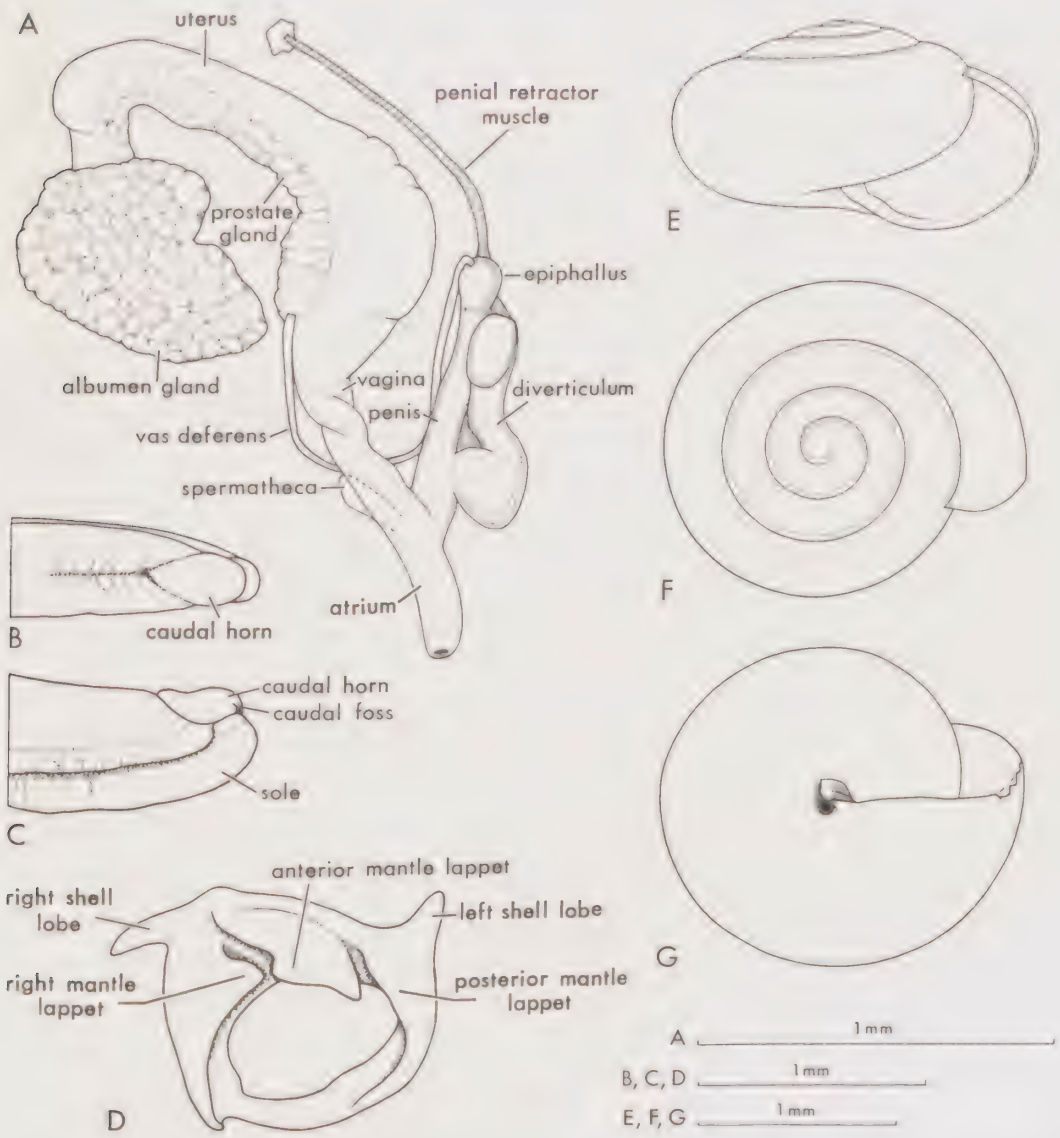

FIG. 3. *Dryachloa dauca* n. sp. A, Reproductive system; B, dorsal view of foot; C, lateral view of foot; D, mantle collar; E-G, holotype, UF 22883.

opening to penis, and low anastomosing ridges in upper portion.

Type locality. Florida, Duval Co., Jacksonville, in a low grassy area along right bank of Ortega River (private residence), (NE 1/4 sec. 5 T 35 R 26 E, Tallahassee). Holotype: UF 22883; collected April-July 1978 by Harry G. Lee. Paratypes: UF 22884 (31 specimens), UF 22885 (2 SEM), UF 22886 (2 SEM), UF 22891 (30), ANSP 350467 (1), MCZ 288513 (1), AMNH 189622 (1), NMNH 784629 (1), UMMZ 250063 (6), FMNH 198744 (1), Harry G. Lee private collection (30); all topotypes.

Distribution. Florida: Duval Co. (type locality); St. Johns Co., 0.5 mi N of Crescent Beach (UF 22818). Specimens from Alabama are tentatively referred to this species. Alabama: Mobile Co., Mobile, vacant lot at Dauphin and Florida streets (UF 22819).

Habitat. This snail lives among roots of grass clusters in areas that are moderately damp. Live specimens were found most frequently after heavy rains, which caused them to crawl to the surface and take shelter on the underside of rocks, boards and logs, where they are easily spotted because of their bright carrot-colored bodies. The species is most frequently found during April through August. Apparently the snail is an annual species. Adults are found during March through May, and then are rapidly replaced by juveniles. Characteristic associates include *Vertigo* sp., *Gastrocopta tappaniana* (C.B. Adams), *Succinea unicolor* Tryon and *Polygyra avara* Say.

RELATIONSHIPS

The classification of the Helicarionidae proposed by Baker (1941: 205-213) and modified by Solem (1966: 22-25) is followed in this paper. A difference between the two systems is that Solem divides the Euconulinae into two tribes, Euconuli and Microcysti, whereas Baker recognizes the latter as a distinct subfamily, the Microcystinae. Earlier classifications placed these subfamilies in the Zonitidae (Pilsbry, 1946).

Dryachloa belongs in the family Helicarionidae, subfamily Euconulinae, tribe Euconuli by virtue of having the umbilicus closed by an internal plug, a well-developed caudal foss overhung by a caudal horn, a tripartite sole, the absence of a stimulator on the female genitalia, the absence of a flagellum or lime sac on the epiphallus, a clavate spermatheca located on the male side of the vagina, and by being oviparous. The location of the spermatheca and the oviparity separate *Dryachloa* from the Microcysti and place it in the Euconuli.

Baker (1941: 212-213) recognized twelve genera in the Euconuli. Four occur in the New World. Eight occur on Indo-Pacific islands and in Southeast Asia. Zilch (1959-1960: 281-282) recognized four additional Indo-Malaysian genera, *Durgellina* Thiele, *Sitalina* Thiele, *Parasitala* Thiele and *Conobycus* Thiele. Baker (1941: 232-233) treated these as synonyms of *Coneuplecta* Moellendorff, an euconulid. The four New World genera are *Euconulus* Reinhardt, *Guppya* Moerch, *Velifera* Binney and *Habroconus* Fisher & Crosse. *Euconulus* is widely distributed in Europe, North America, the Hawaiian Islands and the Society Islands. *Guppya* is widely distributed in eastern North America and Middle America. *Velifera* is known only from Costa Rica, and *Habroconus* is widely deployed in Middle America.

Evolutionary trends within the Euconuli include (1) modification of the shell from a depressed helicoid form with few whorls to conical or dome-shaped with more whorls, (2) trophic specialization through modifications of the radula and (3) reduction or loss of reproductive recognition structures in the genitalia. The modification of the shell reflects trends from being fossorial to being arboreal. Discoidal or depressed species in this subfamily usually are fossorial. Conical or dome-shaped species generally are arboreal. The trophic specializations also correlate with the trends toward arboreal niches and specialized feeding habits. Primitive euconulids have simplified subequal radular teeth arranged in nearly straight transverse rows and bearing three simple cusps on the central and lateral teeth and two to three cusps on the marginals, indicating generalized herbivorous feeding activities. More specialized euconulids have a reduction in the number of marginal tooth rows, multiplication of cusps or secondary denticles on the central and lateral teeth, and a posterior displacement of the lateral and marginal teeth into rows oblique to the central tooth. Evolution of the reproductive system has been characterized by simplification through loss of stimulator organs on the male system.

Dryachloa is more primitive in its morphology than any other euconulid, except perhaps *Guppya*, because of its depressed helicoid shell, its generalized radula, and its generalized reproductive anatomy. It is most closely related to *Guppya* and *Euconulus*. Its close relationship to these two genera suggests that it is a naturally occurring genus in eastern North America and is not an Indo-Pacific or Asiatic introduction. The three genera are differentiated as follows.

Dryachloa. Shell *depressed, with about four whorls*; *embryonic whorls with pitted spiral sculpture* (Fig. 1F); axial striations on latter whorls; *umbilical plug present*; shell-lappets present on mantle collar; prostate nearly as long as uterus; epiphallus without caecum or flagellum; oviparous; laterals asymmetrical; *inner and outer marginals bicuspid.*

Guppya. Shell slightly raised conico-helicoid, four to five whorls; *embryonic whorl with spiral pits that rapidly coalesce into spiral striations* (Fig. 1A); *later whorls without axial striations*; umbilical plug absent; shell-lappets present on mantle collar; *prostate short, confined to upper half of uterus*; *epiphallus with caecoid appendix*; *ovoviviparous*; *lateral teeth symmetrical*; *inner marginals tricuspid*; *outer marginals polycuspid* (Baker, 1922: 45-46; 1928: 6-9).

Euconulus. *Shell dome-shaped*; *five to six whorls*; *embryonic whorl with spiral striations hatched by axial riblets* (Fig. 1B); latter whorls with close axial striations; umbilical plug absent; *shell-lappets absent on mantle collar*; prostate nearly as long as uterus; epiphallus without caecoid appendix; oviparous; lateral teeth asymmetrical; marginals bicuspid (Baker, 1928: 9-11; 1941: 213-220; Pilsbry, 1946: 234-235). (*Euconulus* contains three subgenera, *Euconulus* Reinhardt, *Monoconulus* Baker and *Nesoconulus* Baker, all of which comply with the above definition.)

The shell of *Dryachloa dauca* is similar to *Guppya sterkii* (Dall) in size, shape and sculpture. *G. sterkii* differs most conspicuously by having an imperforate umbilicus. In addition, it has tricuspid marginal teeth typical of *Guppya* (Baker, 1922: 46). Other aspects of its anatomy are unknown. *Dryachloa dauca* is similar in its shell and radula to various species of *Discoconulus* from the Western Pacific and the Orient. However, *Discoconulus* lacks a spermatheca on the vagina and a diverticulum on the penis (Baker, 1941: 227). The shell of *Dryachloa* also resembles *Wilhelminia*. The type species, *W. matildae* Preston (1913: 434), was described from Beilan-Beilan Island, Moluccas, and is known only from the shell. Solem (1959: 94) recorded *W. matildae* from the Solomon Islands and the New Hebrides, and tentatively referred other specimens in the Museum of Zoology, University of Michigan (UMMZ) to this species. We examined two of these lots from Florida Island, Solomon Islands (UMMZ 186146, 186147), three from Espiritu Santo Island, New Hebrides (UMMZ 186143, 186144, 186145), the Moluccas specimens reported by Solem, and four lots from northern Australia (FMNH 182095, 182099, 200428, 200465). The Pacific Island and the Australian specimens agree in all details with Preston's description, but the Moluccas specimens depart significantly in size and sculpture of the embryonic whorls.

Wilhelminia differs from *Dryachloa* in important aspects of the embryonic sculpture. In *Wilhelminia*, the first half embryonic whorl is smooth and the next half bears minute punctae arranged in neat spiral *and* radial rows. In addition, there are uniform radial riblets separating the radial rows of punctae. The punctae do not coalesce on the lower whorls, but remain separated or form short series of pits. Also, the lower whorls have regularly spaced axial striations, not growth wrinkles. On the basis of differences in the embryonic and post-embryonic sculpture, a close relationship (congeneric) between *Wilhelminia* and *Dryachloa* is not tenable.

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AN ANATOMICAL REDESCRIPTION OF *PLEIODON (CAMERONIA) SPEKII* (PELECYPODA: MUTELIDAE: PLEIODONINAE)

William H. Heard and Brian J. Dougherty

ABSTRACT

Several anatomical features of *Pleiodon (Cameronia) spekii*, a freshwater mussel endemic to Lake Tanganyika, are confirmed, others are redescribed and still others are described anew. *P. (C.) spekii* is an unique mutelid because of its pattern of pseudotaxodont hinge dentition, lateral rugae on apically scalloped incurrent and excurrent siphons, dorsal attachment of the inner lamella of the inner demibranchs to the visceral mass for the entire length of the latter, and dimorphic spacing of interlamellar septa (comparatively distant in the outer demibranchs and more dense in the inner demibranchs of both males and females). It is related to *Mutela* by its lack of a triangular sinulus at the posterior end of the hinge plate and by its long presiphonal pallial suture behind the pedal opening. It shares with some *Mutela (Mutela)* and *Aspatharia (Spathopsis)* imperforate, vertically ridgeless septa in the inner, marsupial demibranchs. It and *Mutela (M.) simpsoni* display the unionacean orientation and attachments of the labial palpi, which are posteriorly separated from the inner demibranchs. *P. (C.) spekii* lacks several features previously described as unique to this species, viz., a special sieve plate complex, lateral superior branchial pouches, and vessels in alternating marsupial septa.

INTRODUCTION

Extant freshwater mussels characterized by secondary taxodont (i.e., pseudotaxodont, *fide* Cox, 1969) hinge dentition were long classified in the nominal genus *Iridina* Lamarck 1819 (type species by monotypy: *Iridina exotica* Lamarck 1819). Three monotypic nominal subgenera were customarily recognized: *Iridina* s.s., in which numerous small tubercles occur throughout the length of the hinge plate; *Pleiodon* Conrad 1834 (type by monotypy: *Pleiodon macmurtrei* Conrad 1834 [=*Iridina ovata* Swainson 1823, *fide* Pain & Woodward (1964) and Haas (1969a)]), with taxodont dentition strongly developed throughout the hinge; and *Cameronia* Bourguignat 1879 (type by monotypy: *Iridina (Pleiodon) spekii* S.P. Woodward 1859), in which the taxodont dentition is prominent behind the beaks but is at most weakly developed in front of the beaks.

However, Modell (1964: 85) noted that "... gehen die *Iridina* [*exotica*] unmittelbar aus den grossen Mutelen des Sudan-Gebietes hervor", and, because most *Mutela* possess some tubercles along the hinge (previously noticed by Germain, 1909), Pain & Woodward (1964) synonymized *Iridina* Lamarck 1819 under *Mutela* Scopoli 1777 (first done by Clessin, 1874a, 1874b) and, owing to purportedly unique anatomical features (see below), elevated *Pleiodon* to generic rank.

Pleiodon (sometimes as *Iridina*) have been classified in four subfamilies: Mutelinae s.s. (Thiele, 1934; Modell, 1964, for *Iridina* = *Cameronia* therein); Iridininae Swainson 1840 (Modell, 1942, 1949; = Mutelinae s.s., *fide* Modell, 1964); Aspathariinae Modell 1942 (Modell, 1964, for *Pleiodon*; Starobogatov, 1970); and Pleiodoninae Pain & Woodward 1964 (Pain & Woodward, 1964). Bourguignat (1885) erected the family taxon Iridinidae (recognized by Jousseaume, 1886), and Rochebrune (1904) established Pleiodontidae, whereas all other authors beginning with Adams & Adams (1857) placed *Pleiodon* (and/or *Iridina*) in Mutelidae Gray.

Pain & Woodward (1964) recognized three Recent species: *Pleiodon (P.) ovatus* Swainson 1823 and *P. (P.) waterstoni* Pain & Woodward 1964 of western Africa, and *P. (Cameronia)*

spekii S.P. Woodward 1859, which is endemic to Lake Tanganyika. Verdcourt (1963) recorded *Pleiodon* from Miocene deposits in Kenya, Modell (1964) listed Upper Cretaceous "*Iridina*" (*Iridina* s.s. = *Cameronia* therein) and *Pleiodon* from Egypt, and Haas (1969b) cited *Pleiodon* s.s. from the Upper Pliocene or Pleistocene and *Cameronia* as only Recent. *Pleiodon priscus* von Ihering, from the Cretaceous of Brazil, has been reclassified as a species of Mycetopodidae: *Paxydon* Schumacher (cf. Parodiz & Bonetto, 1963), and the presence of pseudotaxodont dentition in Anthracosiidae: *Pseudomutela verneuili* Amalitzky, from the Permian of Africa, has been interpreted as a case of parallel evolution (Pain & Woodward, 1964).

The anatomies of *Pleiodon* s.s. are unknown, and the soft-part structure of *P. (Cameronia) spekii* was described previously by Pelseneer (1886), Meyer (1958) and Pain & Woodward (1964); according to Pilsbry & Bequeart (1927), Deshayes' (1827) anatomical description of "l'Iridine du Nil" concerned *Mutela (M.) nilotica* (Cailliaud), and Troschel's (1847) account of *Iridina coelestis* Lea concerned *Mutela (M.) rostrata* (Rang). Each of those three accounts on *Pleiodon spekii* differed from the others by containing descriptions of features overlooked by the other workers. There follows a composite description based upon those reports.

Animal with pigmented, papillated, muscular incurrent and excurrent apertures, a pallial suture above the latter but lacking a separate supra-excurrent opening, and a comparatively long pallial suture anterior to the former; diaphragm separating the posterior ends of the branchial and suprabranchial chambers incomplete, with intercommunication accomplished through a sieve plate complex (see below); outer demibranchs with a lateral "superior branchial pouch" resulting from an overfold of the outer lamella dorsal to the sieve plate complex; presence of a densely ciliated "sieve plate complex" that serves to extract food particles from water passing through the branchial chambers; inner demibranchs dorsally attached to the visceral mass along the entire length of the latter, and anteriorly to the labial palpi; marsupia contained in the inner demibranchs; inner demibranchs of gravid but not nongravid females with a vertical ridge on each side of the interlamellar septa, separating the interlamellar space into a water-tube near the inner lamella and a brood space near the outer lamella; septa of gravid animals with numerous minute perforations of irregular distribution; and lacunae (vessels) in the inner demibranchs of gravid females located in alternating septa.

The purposes of this report are to both confirm and correct features in those prior descriptions, to add further details about several structures, and to compare *Pleiodon (Cameronia) spekii* to other mutelacean mussels.

MATERIAL STUDIED

Pleiodon spekii (S.P. Woodward): one gravid female (132 mm long) and one male (117 mm) collected by J.J. and S.T. Landye on 26 September 1974 from Kigoma Bay of Lake Tanganyika, just north of a tributary stream near Kigoma, Tanzania (4°53′ S lat. x 29°39′ E long.). Voucher shells are in the Museum of Zoology, The University of Michigan.

Additional species for comparison: *Aspatharia (Spathopsis) nyassaensis* (Lea), *A. (S.) petersi* (von Martens), dioecious *A. (S.) wahlbergi* (Krauss), *Mutela (Mutela) alata* (Lea) and *M. (M.) simpsoni* Ancey from Malawi; monoecious *A. (S.) wahlbergi* from Zimbabwe (Rhodesia); and *A. (S.) trapezia* (von Martens), *M. (M.) bourguignati* Bourguignat and *M. (M.) rostrata* (Rang) from Lake Victoria (all Mutelacea: Mutelidae); and *Anodontites (Anodontites) carinatus* (Dunker), *A. (A.) trapesialis* form *exotica* (Lamarck) and *A. (A.)* sp. from Colombia, and *A. (A.)* spp. from Mexico (all Mycetopodidae).

METHODS

The Colombian *Anodontites* and *Mutela simpsoni* from Malawi were placed directly into formalin, whereas the animals of the other mutelaceans studied here were narcotized with either menthol crystals (Mexican *Anodontites*) or sodium nembutal (mutelids) and fixed in 10% formalin; all animals were preserved in 70% ethyl alcohol. Gross dissection revealed most features, and histological preparations were

made (see Heard, 1975) in order to identify the sex of each individual and to determine the structure of the demibranchs from frontal and transverse sections. Student's *t*-test was used to statistically interpret differences in septal spacing.

OBSERVATIONS

Mantle, siphons and pigmentation

Mantle sheets conjoined dorsally, and by a pallial suture above the excurrent siphon (without a separate supra-excurrent opening dorsal to it), between the excurrent and incurrent siphons, and anterior to the incurrent siphon for 27.9-28.8% of the length of the animal (Fig. 1). Apex (posterior margin) of both incurrent and excurrent siphons scalloped, presenting a superficial appearance of papillae; lateral (but not medial) surface of both siphons rugose and with rare, small tubercles. Both lateral and medial surfaces of each siphon flecked with moderate concentration of dark brown pigment (less dense on medial surface). Outer (ventral) surface of the pallial suture between the incurrent siphon and the pedal slit with a very dense dusting of dark brown pigment that forms a wide band. (Descriptions of pigmentation are based on preserved specimens, and other pigments and colors, if present in live animals, might have been leached by fixation and preservation.)

Labial palpi

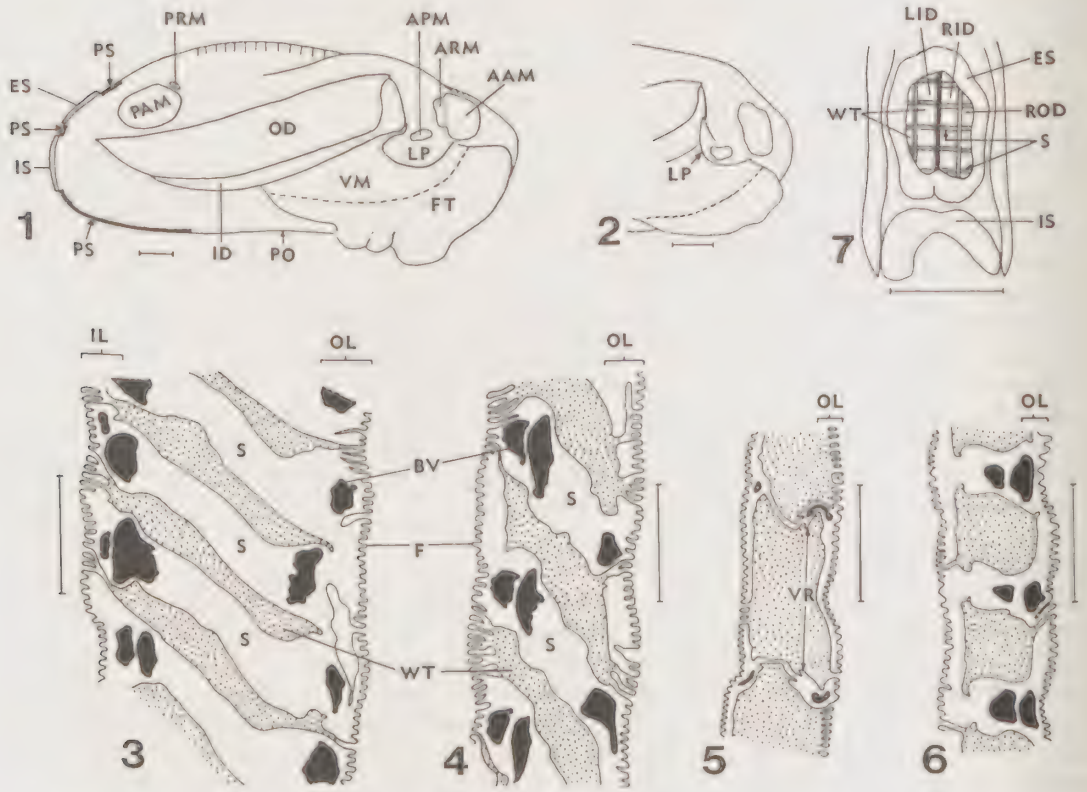
Palps 18.9-21.4% as long as the inner demibranchs, their height 51.8-56.1% of their length. Palpi of *Pleiodon spekii*, as of *Mutela simpsoni*, oriented in an anteroposterior direction (Fig. 1), with posterior 8.7-14.0% of their length free from the apposing mantle sheet and distinctly separated from the inner demibranchs; members of each palp posteriorly free from each other for 13.8-26.8% of their length. Contrasting conditions in the other mutelids examined are: strong dorsal curvature of the palpi (Fig. 2); posterior end nearly contiguous with the anteroventral border of the inner demibranchs; and union of the palp members and also of the outer member with the mantle sheet for their full length.

Demibranchs

All four demibranchs in both specimens of a uniformly dark tan color. Outer demibranchs 0.6-1.6 mm shorter than the inner demibranchs. Outer (ascending) lamella of the outer demibranchs dorsally attached to the inner surface of the apposing mantle sheet for the entire length of the former; dorsal margin of the inner (descending) lamella of each outer demibranch joined to the dorsal margin of the outer (descending) lamella of the inner demibranch of the same ctenidium for its entire length; inner (ascending) lamella of each inner demibranch attached anteriorly to the visceral mass for the length of the latter, and posteriorly (behind the visceral mass) to the inner lamella of the apposing inner demibranch of the other ctenidium for 27.5% of the length of the inner demibranchs of the female and for 38.8% of that of the male. Posterior end of all four demibranchs united to the pallial suture separating the two siphons.

Height of outer and inner lamellae of the outer demibranchs greater than that of their corresponding lamellae in the inner demibranchs (by 1.1-2.2 mm and 1.4-2.4 mm, respectively); height of outer lamella greater than that of the inner lamella in both outer (by 3.8-4.1 mm) and inner demibranchs (3.0-5.4 mm). Height of interlamellar septa in the outer demibranchs greater by 1.5 mm than that of septa in the inner demibranchs of the female, but 0.7 mm shorter than septa in the inner demibranchs of the male.

Interlamellar septa of outer and inner demibranchs of both female and male imperforate; septa in the inner, marsupial demibranchs of the female without vertical ridges (compare Fig. 3 to Fig. 5). Septa comparatively distantly spaced throughout the outer demibranchs of both sexes (female: 16.5 ± 1.3 filaments along each side of 10 water-tubes examined; male:



FIGS. 1, 2. General anatomical features of *Pleiodon (Cameronia) spekii* and *Aspatharia nyassaensis*. FIG. 1. Right side of *P. (C.) spekii*, with the mantle sheet removed from the branchial chamber. FIG. 2. Right side of the anterior end of *A. nyassaensis*, showing the orientation of the labial palpi. Scale for Figs. 1 and 2: 10 mm.

FIGS. 3-6. Camera lucida drawings of frontal sections of part of different demibranchs of *Pleiodon (Cameronia) spekii* and other mutelaceans. FIG. 3. Right inner (marsupial) demibranch of the gravid female *P. (C.) spekii*. FIG. 4. Right outer (non-marsupial) demibranchs of the same female *P. (C.) spekii*. FIG. 5. Right inner (marsupial) demibranch of a nongravid hermaphroditic *Anodontites trapesialis* form *exotica*. FIG. 6. Right inner (marsupial) demibranchs of a nongravid female *Aspatharia nyassaensis*. Scale for Figs. 3-6: 1 mm.

FIG. 7. Dorsoposterior end of the ctenidia (i.e., the four demibranchs behind the visceral mass) of *Aspatharia nyassaensis*, as viewed through the excurrent siphon. (This persepective shows the "sieve plate complex" that Pain & Woodward (1964) reported to be unique to *Pleiodon (Cameronia) spekii*.) Scale: 5 mm.

Abbreviations: AAM, anterior adductor muscle; APM, anterior pedal protractor muscle; ARM, anterior pedal retractor muscle; BV, blood vessel; ES, excurrent siphon; F, filament; FT, foot; ID, inner demibranch; IL, inner lamella; IS, incurrent siphon; LID, left inner demibranch; LP, labial palp; OD, outer demibranch; OL, outer lamella; PAM, posterior adductor muscle; PO, pedal opening; PRM, posterior pedal retractor muscle; PS, pallial suture; RID, right inner demibranch; ROD, right outer demibranch; S, (interlamellar) septum; VM, visceral mass; VR, vertical ridge; WT, water-tube (interlamellar space).

16.0 ± 2.3 filaments/10 water-tubes); septa more densely spaced throughout the inner demibranchs of both sexes (female: 11.8 ± 1.8/10 water-tubes; male: 12.0 ± 1.0/10 water-tubes). (Compare septal spacing in Figs. 3 and 4.) Septal spacing in the outer demibranchs was significantly different from that in the inner demibranchs in both female ($t = 7.86$; $P < .005$)

and male ($t = 6.17$; $P < .005$), but there was no significantly different spacing in the outer demibranchs of female and male ($t = 0.64$; $P > .05$) and also none in septal spacing in the inner demibranchs of female and male ($t = -0.31$; $P > .05$). Lacunae and vessels were found in all septa in both inner (Fig. 3) and outer demibranchs (Fig. 4), and not only in alternating septa.

Diaphragm, sieve plate complex, and lateral superior branchial pouches

The diaphragm separating the posterior region of the branchial chamber from the posterior region of the suprabranchial chamber (i.e., the cloaca) is complete, formed in part by the anterior extension of the pallial suture between the incurrent and excurrent siphons and in part by the posterior ends of the outer demibranchs (attached by the outer lamellae to the mantle).

A unique sieve plate complex, i.e., a structural organization that would contribute to an incomplete diaphragm, was not found in either sex.

Purportedly dorsal to the sieve plate complex, an overfold of the outer (ascending) lamellae of the outer demibranchs that contributes to a lateral superior branchial "pouch" was not confirmed.

Larvae

The single female *Pleiodon spekii* (collected 26 September 1974), several monoecious *Aspatharia wahlbergi* (collected 17 July 1972), several *Mutela bourguignati* (collected 7 October 1974), one *M. rostrata* (collected 10 September 1974) and some *M. simpsoni* (collected 10 December 1965) were gravid, but none contained mature larvae.

DISCUSSION

Discrepancies

The present findings agree with those in prior accounts on *Pleiodon spekii* except for: descriptions of "les orifices palleaux" (Pelseneer, 1886), "Ingestions- und Egestionsoffnung" (Meyer, 1958) and "inhalent and exhalent apertures" (Pain & Woodward, 1964) ornamented with papillae; Meyer's (1958) claims of vertical ridges in the inner, marsupial demibranchs of only gravid and not nongravid females, perforations in these marsupial septa in gravid animals, and "Lakunen-Systems" (circulatory vessels) in alternating marsupial septa; and Pain & Woodward's (1964) report of an unique sieve plate complex and also lateral superior branchial pouches.

Pleiodon spekii lacks the comparatively simple incurrent and excurrent "openings" that are not separated by a pallial suture in non-hyriid Unionacea (e.g., *Anodonta, Caelatura, Elliptio* and *Unio*) and instead possesses the short, muscular siphons that in part characterize Mutelacea: Mutelidae (*Aspatharia* and *Mutela*) but not Mycetopodidae (e.g., *Anodontites*; and *Etheria elliptica* Lamarck, *fide* Heard & Vail, 1976a). In addition, the incurrent opening of Unionacea (see Kokai, 1977) and Mutelacea: Mycetopodidae (Heard & Vail, 1976a; this study) is flanked by at least one row of a variety of kinds of papillae, none of which occur in *P. spekii, Aspatharia* and *Mutela*.

Although Ortmann (1921) reported that vertical ridges on marsupial septa occur only in gravid and not in nongravid Mutelacea (=Mutelidae + Mycetopodidae *sensu* Parodiz & Bonetto, 1963) and Meyer (1958) described that same relationship for *Pleiodon spekii*, our gravid *P. spekii* lacked such ridges (Fig. 3). Moreover, these ridges were found here on marsupial septa of nongravid *Anodontites carinatus*, one species of Mexican *Anodontites*, and some but not all *A. trapesialis* form *exotica* (Fig. 5) and *Aspatharia petersi*. Some but not all gravid *Aspatharia wahlbergi* and *Mutela bourguignati* lacked marsupial septal ridges, whereas septa in the outer, non-marsupial demibranchs of some *Anodontites trapesialis* form *exotica* possessed these ridges. The vertical ridges of the mycetopodids were sharp and well defined, and

those of the mutelids gave the appearance of bulges or swellings in both gravid and nongravid animals (see Fig. 6). Further study of more, seasonal material is needed to interpret the presence and significance of these structures.

Perforated marsupial septa, common in such primitive Unionacea as *Caelatura* of Africa, *Diplodon* of South America, *Hyridella* of Australia and *Pseudodon* of Asia (Heard, 1974), have been illustrated for Mutelidae: *Mutela (Chelidonopsis) hirundo* (see Germain, 1909) and described for *Pleiodon spekii* (Meyer, 1958), but were not found here in *P. spekii*, *Aspatharia*, *Mutela* and *Anodontites*. The unionacean perforations are present in both nongravid and gravid females and are not of seasonal occurrence (Heard, pers. observ.), but the nature of mutelacean perforations is not as well understood.

Meyer's (1958) fig. 2A was claimed to portray lacunae in alternating marsupial septa of *Pleiodon spekii*, but it did not. See Figs. 3 and 4 here for the distribution of vessels in a ctenedium of *P. spekii*, and Figs. 5 and 6 for that of vessels in some other mutelaceans.

Pain & Woodward's (1964: figs. 2, 7) illustrations of the sieve plate complex reveal that this structural organization is not unique to *Pleiodon spekii*. This "complex" simply constitutes the dorsal region of the posterior end of all four demibranchs united to the pallial suture between the incurrent and excurrent siphons, and is common to the other Mutelacea that we have examined (see Fig. 7) as well as to the Unionacea: Hyriidae that lack a perforation in the pallial suture (see McMichael & Hiscock, 1958).

Of the 16 *Aspatharia nyassaensis* that we examined, six (three females and three males) had an overfold of the dorsal part of the outer lamella of just one of the outer demibranchs, a condition that we interpret as due to contraction upon fixation prior to complete narcotization of the animals. Perhaps the same condition occurred in Pain & Woodward's (1964) specimens of *Pleiodon spekii*. If so, there is created no unique lateral superior branchial "pouch", which space in *A. nyassaensis* comprised the dorsal part of the interlamellar space that was forced out of normal position. Finally, an enigma in Pain & Woodward's (1964) figs. 10, 12 and 13 is that the arrow from M.P. ("marsupial pouch") goes to an outer demibranch, to an inner demibranch, and to both an outer and inner demibranch, respectively.

Comparisons to other Mutelidae

The comparatively long presiphonal pallial suture behind the pedal opening, the absence of vertical ridges and perforations associated with the marsupial septa, and the lack of a triangular sinulus at the posterior end of the hinge plate are features of *Pleiodon spekii* that are shared with *Mutela* s.s. and *M. (Chelidonopsis)* (Deshayes, 1827; Rang, 1835; Troschel, 1847; Clessin, 1874a; Germain, 1909; Ortmann, 1910; Pilsbry & Bequeart, 1927; Bloomer, 1932; Mandahl-Barth, 1968; present study). In contrast, the presiphonal pallial suture is short in *Aspatharia (Spathopsis)* and absent in *Aspatharia* s.s., the hinge posteriorly possesses a triangular sinulus in *Aspatharia* s.l., and septal spacing is comparatively distant in all four demibranchs of male, female and hermaphroditic *A. (Spathopsis)* and *Mutela* s.s. (Ortmann, 1918; Pilsbry & Bequeart, 1927; Mandahl-Barth, 1968; present study). The anatomies of Mutelidae: *Arthropteron* and *Chambardia* are unknown.

Features that distinguish *Pleiodon spekii* from other mutelids are pseudotaxodont hinge dentition, rugae on the siphons, attachment of the inner lamella of the inner demibranchs along the full length of the visceral mass, and the peculiar difference in septal spacing between the outer and inner demibranchs of both sexes. Dimorphic septal spacing is widespread among non-margaritiferine Unionacea, with comparatively distant septa in non-marsupial demibranchs and non-marsupial parts of marsupial demibranchs, and densely spaced septa in the marsupia (Ortmann, 1911, 1921; Heard, 1975; Heard & Vail, 1976b); exceptions are *Modellnaia siamensis* Brandt (see Heard & Hanning, 1978), and *Megalonaias* Utterback and *Pseudodon* Conrad (Heard, pers. observ.). The condition in the female *Pleiodon spekii* is equivalent to that in most unionaceans, but the same state in the male is enigmatic. Consequently, examination of more specimens is needed in order to determine the constancy of

this phenomenon. In addition, the *Aspatharia (Spathopsis)* and *Mutela* s.s. examined here possessed a few irregularly distributed tubercles, not papillae and not scalloping, at the apex of the siphons; *M. (Chelidonopsis) hirundo* evidently has simple siphonal apices (see Germain, 1909: 15-17, including fig. 14).

The comparatively wide gap between the palpi and inner demibranchs and also the incomplete attachments of the palps, which features are newly reported here for any mutelid, are features of unionaceans. Moreover, although Ortmann (1921) reported that the palpi of Mutelacea: Mycetopodidae are contiguous with the inner demibranchs, a gap between these structures was found here in all *Anodontites* examined.

Pain & Woodward (1964) expressed doubt that *Pleiodon* s.s., presumably predominantly fluviatile in western Africa (Cosumance River in Senegal, the Niger River drainage and Lake Chad), have the same anatomy of the lacustrine *P. (Cameronia) spekii*. However, as reported here, the sieve plate complex is not an unique structure, and the lateral superior branchial pouches are probably an artifact. Nevertheless, because of dimorphic septal spacing and attachment of the inner demibranchs to the visceral mass in *P. (C.) spekii* and of pseudotaxodont dentition in *Pleiodon* s.l., we retain the subfamilial name Pleiodoninae Pain & Woodward.

Reproduction

Meyer (1958) reported gravid *Pleiodon spekii* from a 17 September collection, although he did not indicate whether mature larvae were present. Our gravid female, collected on 26 September, contained only immature embryos in the upper half of the middle 2/3 of the length of the inner demibranchs. *P. spekii* and possibly also *Aspatharia* s.l. presumably produce haustorial larvae (for description of which in *Mutela bourguignati*, see Freyer, 1961) and neither lasidia of Mycetopodidae (described by Ihering, 1891; Bonetto, 1951; Parodiz & Bonetto, 1963) nor any of the various kinds of unionacean glochidia (see Ortmann, 1911; Parodiz & Bonetto, 1963). The duration of brooding of developing young (i.e., "breeding season" *sensu* Ortmann, 1911; tachytictic = short-term, or bradytictic = long-term) is unknown for any species of Mutelidae.

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A REVIEW OF SACOGLOSSAN DIETS, WITH COMPARATIVE NOTES ON RADULAR AND BUCCAL ANATOMY

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ABSTRACT

Diets of about 60 species of Sacoglossa are summarized, together with radular and buccal anatomy. About 20 species feed on *Caulerpa* spp., about 40 species feed on siphonalean green algae, about 50 species feed on green algae, and only 12 species feed on other food items. However, some species feed on several very different food items, so that food spectra are not as narrow as previously assumed. The most narrow food spectra are found in the bivalved species, and the broadest food spectra are found in some Elysiidae, possibly those with long-term photosynthetic activity of symbiotic chloroplasts. Tooth structure is apparently related to structure of food, with denticulation of any kind representing an adaptation to tough cell walls, calcification, or internal trabeculae. Pharyngeal pouches are found almost exclusively in species feeding on *Caulerpa* spp. This is probably an adaptation to the viscid cell sap found in this genus. Esophageal pouches are found in species feeding on coenocytic algae.

INTRODUCTION

Members of the Sacoglossa (Gastropoda: Opisthobranchia) are known, with few exceptions, to feed on algal cell sap (Macnae, 1954). Information about the actual foods of sacoglossan species is, however, rare. Most authors give records only of the substrate on which the animals were found. This is often, but certainly not always, the same as the food of the species in question. Experimental investigations on sacoglossan food spectra are very few. The most extensive works in this field are: Gascoigne (1956); Hartog (1959); Gonor (1961a,b); Jensen (1975); Usuki (1977); and Clark & Busacca (1978). Occasional notes stating that a certain sacoglossan species was seen feeding on a specific alga are more common, as are statements of a particular alga constituting the food of a sacoglossan species, without information on whether the animal was actually seen feeding or whether the statement was an implication from the fact that the animal was found associated with this algal species in the field. The scattered nature of information on sacoglossan diets has led to the conclusion that sacoglossans have extremely narrow food spectra (Macnae, 1954; Graham, 1955; Gonor, 1961a; Kay, 1968; Greene, 1970a). More recent investigations, however, seem to modify this (Gonor, 1961b; Clark, 1975; Jensen, 1975; Clark & Busacca, 1978).

The rather specialized radula of sacoglossans cannot be adequately described in the same way as other gastropod radulae, since all sacoglossans will have the radular formula 0:1:0 x Y. The sacoglossan radula consists of a dorsal (ascending) and a ventral (descending) limb, ending in an ascus in which old teeth are frequently stored (Gascoigne & Sartory, 1974; Gascoigne, 1977). The number of teeth in each of these sections is of some importance when comparing different species, but, since the number of teeth increases with the age of the animal, it generally does not constitute a species-specific characteristic. In some species the used teeth are discarded from the radular ribbon and heaped up in the ascus, and in these species the number of functional radular teeth may be species-specific, at least in adult animals. But usually only one radula per species has been investigated, so that the utility of this characteristic has been insufficiently analyzed.

The importance of tooth structure in relation to structure of food items was pointed out by Macnae (1954) and has been further stressed by Gascoigne & Sartory (1974). Presence or absence of spinules, bristles and denticles on the teeth, form of cusps, as well as relative

lengths of cusps and bases, are probably related to the structure and texture of food items, but such relationships have never been experimentally clarified. Functions of the radular teeth during feeding are presently unknown, because most sacoglossans are too opaque to permit observations of the radula. Even the most transparent species usually have a muscular (and thus opaque) pharynx. Gascoigne (1977) suggested that the teeth in the descending limb function as the shaft of a lancet when piercing the algal cell walls. The relative size of the pharynx is probably also related to toughness of cell walls and viscosity of cell sap.

The purpose of this study is to compile a survey of sacoglossan diets from the existing literature. Some new records of diets also will be presented, and tooth microstructure and buccal and esophageal anatomy will be related to known food spectra of sacoglossans.

TAXONOMIC REMARKS

Considerable confusion exists concerning placement of genera within the families Stiligeridae and Caliphyllidae. In this paper, taxonomy is taken mainly from Boettger (1962), Baba & Hamatani (1970a,b; 1971) and Gascoigne (1976). The following genera are considered as Caliphyllidae: *Caliphylla, Polybranchia* (= *Phyllobranchillus*), *Mourgona, Cyerce* (Baba & Hamatani, 1971), *Hermaea, Aplysiopsis* (= *Hermaeina*), and *Costasiella* (Gascoigne, 1976). The following genera are considered as Stiligeridae: *Stiliger, Ercolania, Placida, Calliopaea, Limapontia, Olea,* and *Alderiopsis* (Gascoigne, 1976). The type species of *Stiliger, S. ornatus* Ehrenbergh, comes very close to *Placida* (Baba & Hamatani, 1970a), the main difference being that *S. ornatus* has an unarmed penis. However, a number of species previously referred to the genus *Stiliger* have simple or grooved rhinophores, an armed or unarmed penis and blade- or chisel-shaped teeth retained on the radular ribbon. These species probably represent more than two genera, but, as this is not a taxonomic study, only those species earlier transferred to *Placida*, or explicitly said to agree with *P. dendritica* (Alder & Hancock) in anatomy, will be considered as belonging to this genus; the remaining species will be considered as *Stiliger* spp. All species having sabot-shaped teeth, simple or flattened rhinophores and a short penial stylet will be referred to *Ercolania* (Baba & Hamatani, 1970a,b).

A number of *Elysia*, which according to the pattern of dorsal veins were identified as *E. serca* Marcus 1955, have been collected by the author at Key Largo, Florida, U.S.A. However, their radular teeth turned out to be completely smooth, as in *E. clena* Marcus 1970 from Florida (Marcus, 1972b). It thus seems likely that these two species will turn out to be synonymous, but only further investigations on the variability of radular morphology and vein pattern within one species can clarify this. In this paper, the Florida specimens will be referred to *E. serca*, because tooth denticulation is more likely to vary with the type of food eaten than is the pattern of dorsal veins, and because denticulation has already been found to vary in the oldest (smallest) teeth of *E. clena*. Also, if the two species should prove to be synonymous, *E. serca* has priority over *E. clena*.

RESULTS

Of a total of almost 200 known species of Sacoglossa, food has been recorded for about 60 species. Only records explicitly stating that a certain alga is the food of a certain species, or where growth has been detected in the absence of other food material, are considered here as valid records of diets. Only external morphology has been described for many species, but fortunately radular morphology is one of the internal structures most commonly described. Selected tooth shapes are shown in Fig. 1, together with an explanation of terminology. Radular morphology of sacoglossans with known diet is recorded in Tables 1-4. Very few cases exist where the feeding biology has been described but not the radular morphology. The presence of muscular pouches on pharynx and esophagus, which presumably aid in food

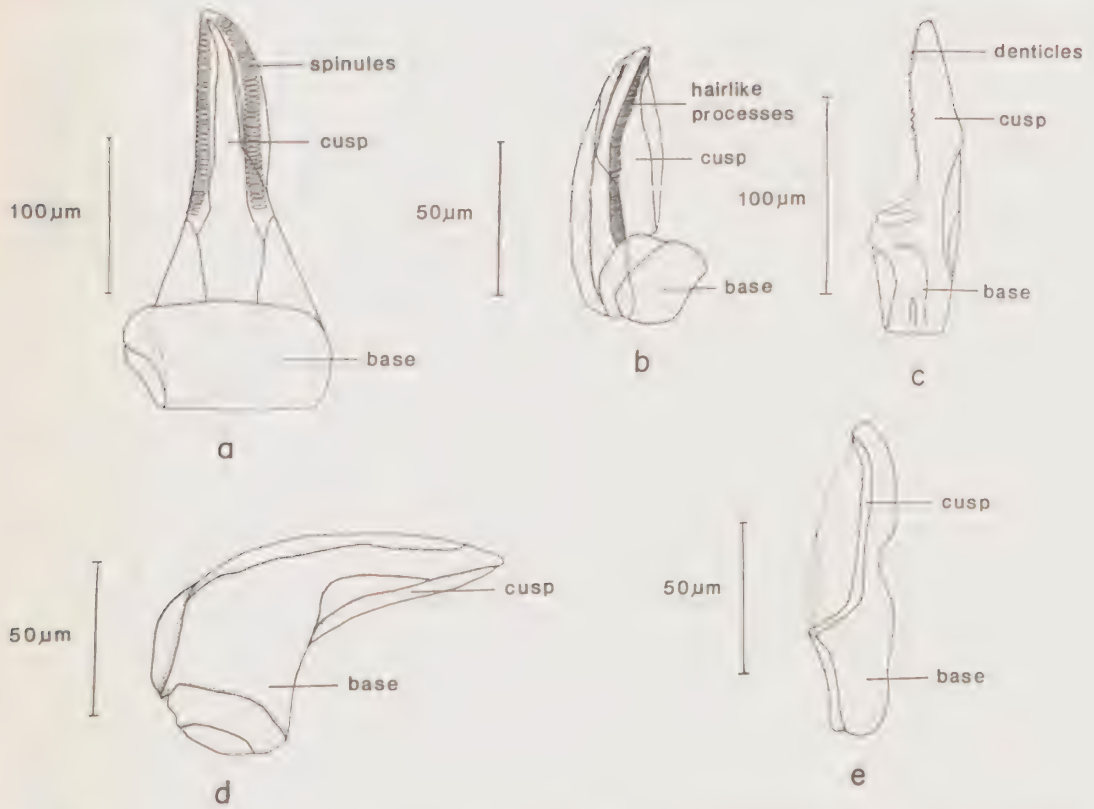

FIG. 1. Tooth shape of five sacoglossans. a, *Ascobulla ulla* (from animal about 1 cm long); b, *Oxynoe* n. sp. (from animal about 5 mm long); c, *Elysia papillosa* (from animal about 1 cm long); d, *Elysia catulus* (from animal about 8 mm long); e, *Ercolania funerea* (from animal about 5 mm long).

uptake, and the relative size of the pharynx are recorded also. However, these structures have not always been described, so these records are not complete.

It can be seen that *Caulerpa* spp. are eaten by about 20 species (Table 1). Radular morphology is known for 18 of these species, and only three species have smooth teeth. *Lobiger souverbiei* Fischer has denticulate teeth in the ascus and the descending limb of the radula, whereas some teeth in the descending and all in the ascending limb are smooth, even of a specimen with a shell length of only 4.15 mm. *Berthelinia typica* (Gatliff & Gabriel) and the two species of *Lobiger* have notched tips on the teeth. Thus only *Ercolania vanellus* (Marcus) has completely smooth teeth, but it is not known whether *Caulerpa verticillata* Agardh actually constitutes its main food or whether the single specimen was accidentally found on this alga by Edmunds (1963). In this connection, it can be mentioned that in Florida *Ercolania fuscata* (Gould) has been found in a habitat very similar to that described by Edmunds (1963) for *E. vanellus*, but *E. fuscata* was feeding on *Cladophora* spp., and it has not yet been observed to feed on *Caulerpa verticillata*.

Algae of the order Siphonales (*Caulerpa, Halimeda, Codium, Bryopsis, Avrainvillea, Penicillus, Chlorodesmis* and *Udotea*) are eaten by about 40 species (Table 2). The majority of the species feeding on *Caulerpa, Halimeda* and *Codium* have denticulate teeth. Denticulate is here taken in the broadest sense, including bristles, spinules and hairlike processes as in *Oxynoe* (Fig. 1b), *Berthelinia*, and *Ascobulla* (Fig. 1a). The interior of *Caulerpa* is traversed by a system of trabeculae (Gascoigne & Sartory, 1974), and most species of *Halimeda* have

TABLE 1. Radular and buccal anatomy of sacoglossans having *Caulerpa* spp. as main food.

Species	Teeth				Pharynx	Esophagus	References
	No. a/d/as*	Length c/b*	Tip	Flanges/edges			
Ascobulla fischeri (Adams & Angas)	25-28*	–	–	with spinules	–	–	Gascoigne & Sartory, 1974
A. ulla (Marcus & Marcus)	7/12/x	190/70 μm	–	with spinules	with muscular pouch	–	pers. observ.
Volvatella pyriformis Pease	23-25*	–	hooked	denticulate	with muscular collar	–	Gascoigne & Sartory, 1974
Julia japonica Kuroda & Habe	?	?	?	?	?	?	Kawaguti & Yamasu, 1966
Berthelinia australis (Burn)	7/35	–	–	with spinules	–	–	Baba, 1961; Gascoigne & Sartory, 1974
B. babai Burn	6/34	–	–	with bristles	–	–	Baba, 1961; Gascoigne & Sartory, 1974
B. caribbea Edmunds	5-6/19-26	–	–	with bristles	with 2 large crops and dorsal pouch	with dorsal diverticulum	Edmunds, 1963
B. ganapati Sarma	7/35	–	–	with bristles	with short, slender crops	–	Sarma, 1975
B. limax (Kawaguti & Baba)	5-7/30-35	–	–	denticulate	–	–	Kawaguti & Baba, 1959

TABLE 1. (Cont.)

Species	Teeth				Pharynx	Esophagus	References
	No. a/d/as	Length c/b	Tip	Flanges/edges			
B. typica (Gatliff & Gabriel)	6/23	–	notched	smooth	–	–	Baba, 1961; Gascoigne & Sartory, 1974
Oxynoe antillarum Mörch	11/18/21	245/120 μm	–	with hairlike processes	muscular with 2 lateral bulges & horseshoe-shaped muscle around ascus	–	Marcus & Marcus, 1970; Bergh, 1900; pers. observ.
O. panamensis Pilsbry & Olsson	?	?	?	?	?	?	Lewin, 1970
O. viridis (Pease)	10/14-22	–	–	with hairlike processes	triturating plates in oral tube & horse-shoe-shaped muscle around ascus	–	Burn, 1966; Gascoigne & Sartory, 1974
Oxynoe n. sp.	16/23/11	200/90 μm	–	with hairlike processes	with large lateral bulges & horseshoe-shaped muscle around ascus	–	Jensen, 1980
Lobiger serradifalci (Calcarra)	–	–	2 notches	smooth	2 lateral & 1 dorsal pouch & horseshoe-shaped muscle	–	Pruvot-Fol, 1954
L. souverbiei Fischer	4-9/8-10/6-12	′280/100 μm	notched	functional & formative smooth, in ascus denticulate	2 lateral muscular thickenings	–	Kay, 1966; Marcus, 1957; Baba, 1974; pers. observ.

TABLE 1. (Cont.)

Species	Teeth				Pharynx	Esophagus	References
	No. a/d/as	Length c/b	Tip	Flanges/edges			
Elysia cauze Marcus	5/32	113/57 μm	–	1-3 μm broad denticles	large, muscular	with dorsal pouch	Marcus, 1957; Marcus & Marcus, 1970
E. tuca [see Table 2]							
Tridachia crispata Mörch	9/9/30	120/70 μm	–	up to 3 μm broad denticles	small	large dorsal pouch	Marcus & Marcus, 1960
Polybranchia viride (Deshayes)	–	130/230 μm	–	coarse denticles, up to 13 μm	large	long pouch	Marcus & Marcus, 1963
Ercolania vanellus (Marcus)	3/5/x	–	–	smooth	–	–	Marcus, 1957

Abbreviations: a = ascending limb of radula; as = ascus; b = base; c = cusp; d = descending limb of radula; x = indefinite number; – = no information available; ? = information not found or unavailable for use.

*a/d/as refers to teeth in ascending limb of radula, followed by number of teeth in descending limb, followed by number of teeth in ascus; c/b refers to length of cusp followed by length of base; 25-28 or 23-25 refers to total number of teeth. This method of tabulation is also used for Tables 2-4.

TABLE 2. Radular and buccal anatomy of sacoglossans having siphonalean diet other than *Caulerpa*.

Species/main food alga	Teeth				Pharynx	Esophagus	References
	No. a/d/as	Length c/b	Tip	Flanges/edges			
Elysia atroviridis Baba/*Codium*	?	?	?	?	?	?	Kawaguti & Yamasu, 1965
E. canguzua Marcus/*Codium*	20	–	–	finely serrulated	–	with muscular pouch	Marcus, 1955
E. fusca Philippi/*Codium*	?	?	?	?	?	?	Schmekel, 1968
E. halimeda Macnae/*Halimeda*	6-9/12/x	–	–	denticulate, possibly 2 rows of denticles	–	–	Macnae, 1954
E. hedgpethi Marcus/*Bryopsis*	8/12/25	120/50 μm	–	finely denticulate, 1-2 μm broad denticles	small	globular muscular, dorsal pouch	Marcus, 1961
E. maoria Powell/*Codium*	?	?	?	?	?	?	Reid, 1964
E. papillosa Verill/*Penicillus*	6/7	ratio c : b = 2.2 : 1	–	coarse denticles, 2-3 μm broad	–	–	Marcus & Marcus, 1967
E. punctata Kelaart/*Codium*	7-9/11-12/x	–	–	smooth	–	–	Macnae, 1954
E. tuca Marcus/*Halimeda*	10/9/x	58/47 μm	–	finely serrulated	no crop	muscular pouch	Marcus & Marcus, 1967; 1970

TABLE 2. (Cont.)

Species/main food alga	Teeth				Pharynx	Esophagus	References
	No. a/d/as	Length c/b	Tip	Flanges/edges			
E. viridis (Montagu)/*Codium*	–	–	–	denticulate	–	muscular pouch	Fretter, 1941;
Tridachia crispata [see Table 1]							
Plakobranchus ocellatus van Hasselt/? *Udotea*	8/7/x	70/70 μm	–	8-10 blunt denticles on each side	–	–	Switzer-Dunlap, 1975
Bosellia mimetica Trinchese/ *Halimeda*	26	tot. 40-45 μm	–	denticulate	large sessile ingluvies	–	Marcus & Marcus, 1970; Marcus, 1973
Caliphylla mediterranea Costa/ *Bryopsis*	–	–	–	smooth	with 2 lateral pouches	with muscular pouch	Marcus, 1958; Marcus & Marcus, 1970
Costasiella lilianae (Marcus)/ *Avrainvillea*	8-9/9-10	–	–	smooth	–	–	pers. observ.
Cyerce antillensis Engel/ *Penicillus*	–	39/26 μm	–	finely denticulate	pharyngeal pouch larger than pharynx	–	Marcus & Marcus, 1963; 1970
C. nigra Bergh/*Chlorodesmis*	–	–	–	denticulate	–	–	Bergh, 1873
Placida capensis (Macnae)/ *Codium*	30 + x	–	–	smooth	–	–	Macnae, 1954

TABLE 2. (Cont.)

Species/main food alga	Teeth				Pharynx	Esophagus	References
	No. a/d/as	Length c/b	Tip	Flanges/edges			
P. dendritica (Alder & Hancock/*Codium*	–	–	–	smooth	–	with crop	Pruvot-Fol, 1954
P. kingstoni Thompson/ *Bryopsis*	–	–	–	smooth	–	–	Thompson, 1977; pers. observ.
P. viridis Trinchese/ *Bryopsis*	–	–	–	smooth	–	–	Pruvot-Fol, 1954
Limapontia capitata [see Table 3]							

Abbreviations: a = ascending limb of radula; as = ascus; b = base; c = cusp; d = descending limb of radula; x = indefinite number; – = no information available; ? = information not found or unavailable for use.

conspicuous encrustations of calcium carbonate (Taylor, 1972), which might render them very difficult to penetrate and suck cell sap from. Such obstacles are not found in *Codium*, but this genus, like *Acetabularia* and *Halicoryne*, has mannan as its structural cell wall polysaccharide, and no microfibrillar structures have been found (Percival, 1968). The structural polysaccharide of the cell walls of *Caulerpa* and *Halimeda* is xylan, the same material as in *Bryopsis, Udotea, Chlorodesmis* and *Pseudodichotomosiphon* (Percival, 1968). However, most species that have *Bryopsis* as their main food have smooth teeth. This algal genus has thin flexible filaments that can be grasped individually by most sacoglossans. The sacoglossans feeding on *Penicillus* all have denticulate teeth, and the filaments of this algal genus are relatively thin but, like *Halimeda*, more or less encrusted with calcium carbonate. *Acetabularia*, possibly eaten by *Elysia timida* Risso, is also calcified.

Possibly all three species of *Bosellia* (*B. mimetica* Trinchese, *B. marcusi* Marcus and *B. corinnae* Marcus) feed on *Halimeda*, since they have been found exclusively on this algal genus (Marcus, 1973) and their external appearances are very similar to a segment of *Halimeda*. However, their tooth structures are very different (Marcus, 1973), and it must be suspected that their modes of feeding are also very different. *B. corinnae* has teeth four times the length of the teeth of the other two species, and *B. mimetica* has large pharyngeal muscular diverticula ("sessile ingluvies") which are not found in the other two species.

The teeth of *Costasiella lilianae* (Marcus) are all of the same size (pers. observ.). This probably reflects the fact that *Avrainvillea* has uniformly very thin filaments and, if the teeth were much larger, they would be broader than the algal filaments. In most other sacoglossans, tooth size increases with increasing size of the animal, and small animals will eat filaments of a different diameter than will the adults. This is seen for instance in *Elysia punctata* Kelaart and *Placida capensis* (Macnae), in which a positive correlation was found between the size of the animals and the diameter of the *Codium* utricles they fed on (Macnae, 1954), and in *Berthelinia babai* (Burn), where the small animals fed on stolons and rhizoids and the adults on the sword-like edges of *Caulerpa scalpelliformis* (Brown ex Turner) (Burn, 1960). *Costasiella lilianae* has direct development (Clark & Goetzfried, 1978) and thus hatches at a relatively large size. This may also account for the lack of small juvenile teeth.

Cladophorales (*Cladophora, Chaetomorpha, Rhizoclonium, Urospora*) are eaten by 13 sacoglossans (Table 3). They almost all have smooth sabot-shaped teeth (*Ercolania* (Fig. 1e) and *Limapontia*). The cell walls of Cladophorales contain regularly crossing microfibrillae of cellulose (Christensen, 1966), and it is possible that these microfibrillae can clog denticles, but *Aplysiopsis smithi* (Marcus) has coarsely denticulate, sabot-shaped teeth and feeds exclusively on Cladophorales. The sabot-shaped teeth may be an adaptation to scoop in the large reticulate chromatophore found in these algae (Christensen, 1966).

Greene (1970a) pointed out that algae eaten by sacoglossans must have large cells or be coenocytic to yield an adequate amount of cell sap per puncture. This is found almost exclusively in the four chlorophyte orders Siphonales, Dasycladales, Siphonocladiales and Cladophorales. All green algae presently known to be eaten by sacoglossans belong to these four orders (*Acetabularia* and *Batophora* belong to Dasycladales and *Valonia* and *Cladophoropsis* belong to the Siphonocladiales). Other algae eaten by sacoglossans (Table 4) either have large cells (*Griffithsia*) or are coenocytic (*Vaucheria*). Very few sacoglossans eat parenchymatic (*Padina*) or polysiphonaceous (*Polysiphonia*) algae. Anthophyta, which must be considered parenchymatic, are likewise eaten by very few sacoglossans, and the species eaten (*Zostera, Halodule* and possibly *Thalassia*) have very large cells. In this connection, it is interesting to note that the teeth of *Elysia catulus* (Gould) (Fig. 1d), *E. serca* and *E. clena* are of a similar shape, which differs from all other sacoglossans, the bases being at almost right angles to the cusps (Marcus, 1970). The former two species feed on *Zostera* and *Halodule* respectively (Clark, 1975; Jensen, 1978), and *E. clena* has usually been found associated with *Thalassia* (Marcus & Hughes, 1974). Like the Cladophorales, Anthophyta have cellulose

microfibrillae in their cell walls, but, of these three *Elysia* species, *E. catulus* has smooth teeth, whereas tooth denticulation of the other two species apparently is variable (Marcus, 1972b; pers. observ.).

Opisthobranch eggs, which are eaten by three sacoglossans (Table 4), are in many respects similar to monosiphonaceous algae such as *Chaetomorpha*. They consist of a more or less spirally coiled string of eggs placed one after the other. The most significant difference is the "jelly" usually surrounding the egg-string, and for which no algal parallel can be found. *Olea hansineensis* Agersborg probably represents the highest degree of adaptation to this food item, having a very much reduced radula (often recorded as absent) (Gascoigne, 1975), whereas the radulae of *Stiliger vesiculosus* (Deshayes) and *Calliopaea oophaga* Lemche have not undergone such profound specialization (Pruvot-Fol, 1954; Gascoigne & Sartory, 1974; Gascoigne & Sigurdsson, 1977). In *Calliopaea oophaga*, tooth width suddenly increases in tooth no. 7, and it is suggested that this may be the stage at which oophagy begins (Gascoigne & Sartory, 1974).

The food spectra of a number of sacoglossans are shown in Table 5. This table may be incomplete, because some investigators have not tried to feed their animals more than one algal species. Still, the most narrow food spectra are found in the bivalved species and *Lobiger* spp., which feed on only one or occasionally two species of *Caulerpa*. Perhaps the species feeding on Anthophyta also have extremely narrow food spectra, but these species are very poorly investigated.

The broadest food spectra are found in various species of Elysiidae, possibly those with long-living symbiotic chloroplasts, but the existing literature on that subject is too scarce to really establish such a correlation. In a number of Elysiidae, i.e., *Elysia viridis* (Montagu) (Hinde & Smith, 1972), *Tridachia crispata* Mörch (Trench & Ohlhorst, 1976), *Tridachiella diomedea* (Bergh) (Trench et al., 1969) and *Plakobranchus ianthobapsus* Gould (Greene, 1970b), photosynthetic activity has been shown to persist for one to three months after the animals had been removed from their food. In fact, *P. ianthobapsus* has never been found associated with any alga (Greene, 1970a), and feeding experiments have been inconclusive (Switzer-Dunlap, 1975). Photosynthesis has been demonstrated in some non-elysiid species, but not for such long intervals, e.g., *Hermaea bifida* (Montagu), 7-8 days (Taylor, 1971), and *Limapontia depressa* Alder & Hancock, $\leqslant$ 2 weeks (Hinde & Smith, 1974). Despite several experiments, it has not been possible to demonstrate photosynthesis in *Berthelinia chloris* Dall, *Oxynoe antillarum* Mörch (Muscatine & Greene, 1973), *Aplysiopsis smithi* (Greene, 1970a), *L. capitata* (Müller) or *Alderia modesta* (Loven) (Hinde & Smith, 1974).

Probably duration of photosynthetic activity is a quality of the chloroplasts rather than of the sacoglossans. Thus the chloroplasts of *Codium* and *Caulerpa* spp. have extremely tough membranes (Giles & Sarafis, 1974; Trench & Ohlhorst, 1976). Muscatine & Greene (1973) noted that none of the symbiotic chloroplasts from *Elysia, Tridachia* and *Plakobranchus* contained pyrenoids and that pyrenoids are absent from *Codium* chloroplasts.

Calvert et al. (1976) divided the *Caulerpa* spp. into seven groups on the basis of chloroplast types. The most primitive chloroplasts contain a large pyrenoid and the most advanced ones contain neither pyrenoid nor starch grains. The most primitive species of *Caulerpa* are eaten by only three species of sacoglossans, all bivalved and all Pacific species. It is noticeable that these primitive species, *C. simpliciuscula* (Turner), *C. geminata* Harvey and *C. okamurai* Weber-van Bosse, all have the same growth form as *C. racemosa* (Forsskål), which is probably the most widespread food species of sacoglossans, being eaten by six out of 16 species (Tables 1 and 5). The chloroplasts of *C. racemosa* are of an intermediate type with no pyrenoid and a number of small starch grains. *C. cupressoides* (West) and *C. paspaloides* (Bory) also have chloroplasts of intermediate type, whereas the chloroplasts of the remaining *Caulerpa* spp. eaten by sacoglossans are of the most advanced type. *C. sertularioides* (Gmelin) is probably the most widely used of these, being eaten by five out of 16 species (Tables 1

TABLE 3. Radular and buccal anatomy of sacoglossans having green algae other than Siphonales as food.

Species/main food alga	Teeth				Pharynx	Esophagus	References
	No. a/d/as	Length c/b	Tip	Flanges/edges			
Elysia chlorotica Gould/ *Cladophora*	6/11/4	–	–	smooth	small	with glandular pouch	Marcus, 1972a
E. timida Risso/*Acetabularia*	5/7/x	–	–	denticulate	–	–	Swennen, 1961
E. viridis [see Table 2]							
Aplysiopsis smithi (Marcus)/ *Rhizoclonium*	6/31	148/42 μm	–	denticles 3 μm broad	–	no pouches	Marcus, 1961
Ercolania boodleae (Baba)/ *Chaetomorpha*	4-6/5-7/x	–	–	smooth	–	no pouches	Baba & Hamatani, 1970b
E. coerulea Trinchese/ *Valonia*	2/6/8	–	–	smooth	enormous	–	Marcus & Marcus, 1960
E. funerea (Costa)/ *Chaetomorpha*	20 a + d/20	145/45 μm	–	smooth	–	–	Marcus & Marcus, 1970
E. fuscata (Gould)/ *Cladophora*	4/11/25	–	–	smooth	large, muscular	with muscular pouch	Marcus, 1958

TABLE 3. (Cont.)

Species/main food alga	Teeth				Pharynx	Esophagus	References
	No. a/d/as	Length c/b	Tip	Flanges/edges			
E. gopalai (Rao)/ *Chaetomorpha*	6/7/20	tot. 125 µm	–	smooth	muscular	no pouches	Rao, 1937
E. nigra (Lemche)/ *Chaetomorpha*	4-5/5/x	–	–	smooth	–	–	Lemche, 1935
E. viridis (Costa)/ *Chaetomorpha*	–	–	–	smooth	–	–	Trinchese, 1872
Limapontia capitata (Müller)/ *Cladophora*	–	–	–	smooth	1/6 the length of animal	no pouches	Gascoigne, 1956
L. cocksi (Alder & Hancock)/ *Cladophora*	3/8/x	80/50 µm	–	smooth	1/6 the length of animal	no pouches	Gascoigne, 1956
L. depressa [see Table 4]							

Abbreviations: a = ascending limb of radula; as = ascus; b = base; c = cusp; d = descending limb of radula; x = indefinite number; – = no information available.

TABLE 4. Radular and buccal anatomy of sacoglossans having food other than green algae.

Species/main food item	Teeth				Pharynx	Esophagus	References
	No. a/d/as	Length c/b	Tip	Flanges/edges			
Elysia catulus Gould/*Zostera*	11/18-19/x	100/34 μm	–	smooth	large, with muscles surrounding descending limb	with muscular pouch	Marcus, 1972a
E. evelinae Marcus/diatoms	10 a + d/8	–	thickened	smooth with thickened borders	with 2 lateral muscular pouches	–	Marcus, 1957; Jensen, 1978
E. serca Marcus/*Halodule*	7/20	–	–	± denticulate	enormous	no pouches	Marcus, 1955; Jensen, 1978
Tridachiella diomedea (Bergh)/ *Padina*	–	–	–	smooth	–	–	Marcus, 1967
Hermaea bifida (Montagu)/ *Griffithsia*	–	–	–	smooth	–	–	Pruvot-Fol, 1954
H. vancouverensis O'Donoghue/ diatoms	–	–	–	smooth	–	–	Williams & Gosliner, 1973

TABLE 4. (Cont.)

Species/main food item	Teeth				Pharynx	Esophagus	References
	No. a/d/as	Length c/b	Tip	Flanges/edges			
Stiliger fuscovittatus Lance/ *Polysiphonia*	7/23/4	–	–	smooth	–	–	Lance, 1962
S. vesiculosus (Deshayes)/ opisthobranch eggs	5/12	–	–	smooth	–	–	Pruvot-Fol, 1954
Calliopaea oophaga Lemche/ opisthobranch eggs	–	–	–	smooth	small	no pouches	Gascoigne & Sigurdsson, 1977
Olea hansineensis Agersborg/ opisthobranch eggs	0/4	–	–	smooth	–	–	Gascoigne, 1975
Limapontia depressa Alder & Hancock/ *Vaucheria*	–	–	–	smooth	1/10 the length of animal	–	Gascoigne, 1956
Alderia modesta (Loven)/ *Vaucheria*	–	–	–	smooth	1/20 the length of animal	with swelling in front of stomach	Gascoigne, 1956

Abbreviations: a = ascending limb of radula; as = ascus; b = base; c = cusp; d = descending limb of radula; x = indefinite number; – = no information available.

TABLE 5. Sacoglossan food spectra. Food items eaten only in the laboratory are shown in brackets.

Species	Diet	References
Ascobulla fischeri	stolons of *Caulerpa* spp.	Gascoigne & Sartory, 1974
A. ulla	*Caulerpa racemosa* (Forsskål)	this study
Volvatella pyriformis	stolons of *Caulerpa* spp.	Gascoigne & Sartory, 1974
Julia japonica	*Caulerpa ambigua* Okamura	Kawaguti & Yamasu, 1966
Berthelinia australis	*Caulerpa simpliciuscula* (Turner)	Burn, 1960
B. babai	*Caulerpa scalpelliformis* (Brown), *C. geminata* Harvey	Burn, 1960, 1965; Gascoigne & Sartory, 1974
B. caribbea	*Caulerpa verticillata* Agardh	Grahame, 1969
B. ganapati	*Caulerpa racemosa*	Sarma, 1975
B. limax	*Caulerpa okamurai* Weber-van Bosse	Kawaguti & Baba, 1959
B. typica	*Caulerpa brownii* (Agardh)	Burn, 1965
Oxynoe antillarum	*Caulerpa racemosa* [*C. sertularioides* (Gmelin)]	Marcus & Hughes, 1974; Clark & Busacca, 1978; pers. observ.
O. panamensis	*Caulerpa sertularioides*	Lewin, 1970
O. viridis	*Caulerpa* spp.	Gascoigne & Sartory, 1974
Oxynoe n. sp.	*Caulerpa paspaloides* (Bory), *C. cupressoides* (West) [*C. sertularioides*]	Jensen, 1980
Lobiger serradifalci	*Caulerpa prolifera* (Forsskål)	Gonor, 1961a
L. souverbiei	*Caulerpa racemosa*	this study
Elysia atroviridis	*Codium fragile* (Suringar) Hariot	Kawaguti & Yamasu, 1965
E. canguzua	*Codium* sp.	Marcus, 1955
E. catulus	*Zostera marina* (Linnaeus)	Clark, 1975
E. cauze	*Caulerpa ashmeadii* Harvey, *C. racemosa*, *C. sertularioides* [*C. cupressoides*, *C. mexicana* Sonder, *C. paspaloides*]	Clark & Busacca, 1978; pers. observ.
E. chlorotica	*Cladophora* spp., *Vaucheria* spp.	Franz, 1968; Clark, 1975
E. evelinae	*Biddulphia* sp., ?*Dictyota*	this study; Marcus, 1957
E. fusca	*Codium* sp.	Schmekel, 1968
E. halimeda	*Halimeda cuneata* Hering, *Codium* spp.	Macnae, 1954

TABLE 5. (Cont.)

Species	Diet	References
E. hedgpethi	*Codium fragile, Bryopsis corticulans* Setchell	Greene, 1970a
E. maoria	*Codium*	Reid, 1964
E. papillosa	*Penicillus* spp.	this study
E. punctata	*Codium* spp.	Macnae, 1954
E. serca	*Halodule wrightii* Ascherson, ? *Ulva lactuca* Linnaeus	this study; Horsoe, 1956
E. timida	?*Acetabularia* sp.	Schmekel, 1968
E. tuca	*Halimeda* spp., *Caulerpa sertularioides* [*C. mexicana, C. racemosa, Avrainvillea nigricans* Decaisne, *Udotea* sp.]	Clark & Busacca, 1978
E. viridis	*Codium* spp., *Bryopsis plumosa* (Hudson), *Chaetomorpha linum* (Müller)	Fretter, 1941; Rasmussen, 1973; pers. observ.
Plakobranchus ocellatus	? *Udotea*, ? *Chlorodesmis*	Switzer-Dunlap, 1975
Bosellia mimetica	*Halimeda tuna* (Ellis & Solander)	Portmann, 1958
Tridachiella diomedea	*Padina* sp.	Bertsch & Smith, 1973
Tridachia crispata	*Halimeda* sp., *Bryopsis plumosa, Penicillus* sp., *Batophora* sp., *Caulerpa verticillata*	Clark & Busacca, 1978; pers. observ.
Caliphylla mediterranea	*Bryopsis* sp.	Brüel, 1904
Cyerce antillensis	*Penicillus* spp., *Halimeda* spp.	this study
C. nigra	*Chlorodesmis comosa* Bailey & Harvey	Miller, 1969
Polybranchia viride	? *Caulerpa* spp.	Bertsch & Smith, 1973
Aplysiopsis smithi	*Rhizoclonium* sp., *Cladophora* sp., *Chaetomorpha* sp., *Urospora* sp.	Gonor, 1961b; Greene, 1970a
Hermaea bifida	*Griffithsia flosculosa* (Ellis)	Taylor, 1971; Kremer & Schmitz, 1976
H. vancouverensis	*Isthmia nervosa* Kützing	Williams & Gosliner, 1973
Costasiella lilianae	*Avrainvillea nigricans*	Clark & Busacca, 1978; pers. observ.
Placida capensis	*Codium stephensiae* Dickinson	Macnae, 1954
P. dendritica	*Codium* sp., *Bryopsis plumosa*	Brüel, 1904; Fretter, 1941; Greene, 1970a

TABLE 5. (Cont.)

Species	Diet	References
P. kingstoni	*Bryopsis* sp.	this study
P. viridis	*Bryopsis plumosa*	Schmekel, 1968; Monselise & Mienis, 1977
Calliopaea oophaga	eggs of *Philine denticulata* (Adams) and *Retusa truncatula* (Bruguière)	Lemche, 1974
Stiliger fuscovittatus	*Polysiphonia pacifica* Hollenberg	Lance, 1962
S. vesiculosus	eggs of *Favorinus branchialis* (Rathke)	Haefelfinger, 1962
Olea hansineensis	eggs of *Haminoea virescens* (Sowerby), *Aglaja diomedea* (Bergh), *Gastropteron pacificum* Bergh [*Archidoris montereyensis* (Cooper), *Hermissenda crassicornis* (Eschscholtz), *Dendronotus iris* Cooper]	Crane, 1971
Ercolania boodleae	*Chaetomorpha aerea* Kützing, *C. moniligera* Kjellman, *Cladophora* spp.	Usuki, 1977
E. coerulea	*Valonia* sp.	Schmekel, 1968
E. funerea	*Chaetomorpha* spp., *Cladophora* spp.	this study
E. fuscata	*Cladophora* spp., *Chaetomorpha linum*	Clark, 1975; pers. observ.
E. gopalai	*Chaetomorpha* sp.	Rao, 1937
E. nigra	*Chaetomorpha linum*	Rasmussen, 1973; pers. observ.
E. vanellus	?*Caulerpa verticillata*	Edmunds, 1963
E. viridis	*Chaetomorpha* sp.	Trinchese, 1872
Limapontia capitata	*Cladophora* spp., *Chaetomorpha linum* [*Bryopsis plumosa*]	Gascoigne, 1956; Jensen, 1975
L. cocksi	*Cladophora rupestris* (Linnaeus)	Gascoigne, 1956
L. depressa	*Vaucheria* spp., *Rhizoclonium riparium* (Roth)	Gascoigne, 1956; Hartog, 1959
Alderia modesta	*Vaucheria* spp.	Evans, 1953; Hartog, 1959

? = uncertain whether this food item is actually eaten by the sacoglossan species.

and 5). Most of these species have growth forms with rather thin filaments (Charoideae, Filicoideae), but some have broad "leaves" (Calvert et al., 1976). It may be noted that *Vaucheria compacta* Collins, which is eaten by *Alderia modesta*, *Limapontia depressa* and

Elysia chlorotica Gould, contains pyrenoids (Hartog, 1959), and short term photosynthetic activity has been demonstrated in the latter two species (Hinde & Smith, 1974; West, 1977). Pyrenoids are of universal occurrence in Cladophorales (Taylor, 1972), but photosynthesis has not yet been detected in any species feeding on these algae.

DISCUSSION

Since *Caulerpa* spp. constitute the food of the most primitive sacoglossans and also of the largest number of species, it must be concluded that this genus is the original food of sacoglossans. This was also noted by Gonor (1961a) and Kay (1968). Kay suggested that some nutritional factor found only in *Caulerpa* was necessary for the sacoglossans, and that the species that fed on other algae obtained this factor from symbiotic zoochlorellae or zooxanthellae. These have now been shown to be chloroplasts of the algae eaten by the sacoglossans (Kawaguti & Yamasu, 1965; Greene, 1970a). However, no one has proved that the photosynthetic products translocated to sacoglossans are essential for the animals. In *Tridachia*, most of the photosynthetically fixed carbon can be found in the pedal mucus gland (Trench, 1973), but all sacoglossans can secrete large amounts of mucus, even those which do not retain symbiotic chloroplasts, e.g., *Limapontia capitata* and *Alderia modesta* (pers. observ.). Clark & Busacca (1978) mentioned chlorophyll half life of 15 days for *Oxynoe antillarum*, but they also noted a high mortality in the starved animals, so the retention of chlorophyll in itself is apparently not proof for the existence of a nutritional benefit for the host animal. Clark et al. (1979) have shown that light is essential for growth of juvenile *Elysia cauze*, but this species feeds on *Caulerpa* spp. and also has a rapid chlorophyll turnover time (Clark & Busacca, 1978), so, even though photosynthesis seems to be essential, no satisfactory explanation can be given as to why.

Greene (1970a) summarized foods of 38 species and found that 56% fed on Siphonales. This is confirmed by the present study, with about 67% of the species feeding on Siphonales, green algae eaten by about 85%, and only 20% using other foods. However, some species feed on several very different food items (hence the total of 105%), and food spectra are not so narrow as previously assumed. The ability to phagocytize viable chloroplasts may be of widespread occurrence among the sacoglossans. The retention time varies greatly, but this may be a characteristic of the chloroplasts rather than of the sacoglossans.

Denticles, spinules and bristles on the teeth presumably represent structural adaptations to food items with tough cell walls, trabeculae and encrustations of calcium carbonate. The majority of sacoglossans feeding on *Codium* also have denticulate teeth, although the denticles are finer than those of the sacoglossans feeding on *Caulerpa, Halimeda* or *Penicillus*. Most species of *Codium* have very densely set utricles, so that it is not possible for the sacoglossans to grasp an individual utricle. Rather, *Codium* is treated as a flat leaf, and it could be argued that the majority of species feeding on flat food items have denticulate teeth, whereas those feeding on filamentous algae other than *Caulerpa* have smooth teeth. However, species feeding on *Penicillus* also have denticulate teeth, and the filaments of this alga are thin enough to be grasped individually, so it must be concluded that calcification and internal trabeculae are the major factors necessitating denticulation of teeth, and that the cell walls of *Codium* for some unknown reason are tougher than those of *Bryopsis*.

As food spectra radiate from *Caulerpa*, tooth structure is altered so that the primitive teeth of the shelled sacoglossans, with spinules or bristles on the flanges, evolve into teeth with denticles on the cutting edge as in many *Elysia* spp. (Fig. 1c), *Aplysiopsis, Cyerce,* etc. The completely smooth teeth of some *Elysia* spp., *Hermaea, Caliphylla, Placida,* etc., are evolutionarily more advanced. The smooth sabot-shaped teeth of *Ercolania* (Fig. 1e) and *Limapontia* presumably represent the highest evolutionary stage. It can be seen that smooth teeth are found in Elysiidae, Caliphyllidae and Stiligeridae, even though the latter two families

are supposed to have evolved from a different line than the Elysiidae (Boettger, 1962). Accordingly, it must be concluded that smooth teeth are a convergent adaptation to similar food structure, and it can be seen that smooth teeth in Elysiidae and Caliphyllidae are found mostly in species feeding on non-siphonalean algae.

The bases of the sacoglossan teeth may reflect phylogenic relationships within this order. Generally, Oxynoidae and Elysiidae have teeth with short bases, whereas Lobigeridae, Caliphyllidae and Stiligeridae have teeth with long bases (> 1/3 of the total tooth length). However, there are exceptions to this. For instance, *Elysia tuca* has teeth with relatively long bases (Marcus & Marcus, 1967), but *Aplysiopsis smithi* and *Cyerce cristallina* (Trinchese), both presently referred to Caliphyllidae, have teeth with short bases (Marcus, 1961; Marcus & Marcus, 1970), and possibly this characteristic is more dependent on food and mode of feeding than on phylogeny.

Muscular pharyngeal pouches or sessile ingluvies are found almost exclusively in species feeding on *Caulerpa* spp. This may be an adaptation to the presence of internal trabeculae in this genus or to the viscid cell sap (Gonor, 1961a; pers. observ.). Esophageal pouches are found in many species and probably are an adaptation to sucking in large amounts of cell sap with each piercing of the cell wall. In species feeding exclusively on cellular food items, muscular pouches may be completely absent, e.g., in *Aplysiopsis smithi* (Marcus, 1961), *Limapontia capitata* (Fretter, 1941), *Elysia serca* (Marcus, 1955) and *E. chlorotica* (Marcus, 1972a).

As previously mentioned, food is known only for about 30% of the sacoglossan species. Therefore, it is important that future investigations of field associations of sacoglossans and potential food items also include laboratory observations of whether these items are actually eaten by the animals. The effect of sacoglossan feeding can often be seen as discolored spots or streaks on the food plant (pers. observ.), but it takes a trained observer to distinguish these "feeding tracks" from other abnormalities in the plants, such as zoospore release, disease and feeding activity of other animals (halacarids, ostracods and others). Therefore, laboratory observations of feeding will be the most conclusive method to establish the food spectra of sacoglossans and, since most sacoglossans are easily kept in small containers at room temperature (approximately 20°C), it should be fairly easy to make such observations.

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BRIEF COMMUNICATIONS

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FIRST SUCCESS IN REARING HATCHLINGS OF THE SQUID *LOLIGO PEALEI* LESUEUR 1821. – The common Atlantic coast squid *Loligo pealei* Lesueur 1821 (Myopsida: Cephalopoda) is important to commercial fisheries (Voss, 1973) and as a source of giant axons for neurophysiological research (Arnold et al., 1974). Despite numerous attempts over the past 100 years to rear the hatchlings from eggs, no success beyond a few days has been attained (Verrill, 1880; Williams, 1909; Arnold et al., 1974). The hatchlings are very small (mean mantle length (ML) of 1.5 mm) and they still possess an internal yolk supply that meets their post-hatching metabolic requirements for a few days. After the yolk is exhausted, they must begin feeding on live and moving planktonic food. Determining and supplying the appropriate type and size of food at this period is the first critical step in rearing hatchlings beyond the post-yolk-sac stage. The present communication reports the first successful rearing of laboratory-spawned *L. pealei*.

Hatchlings were obtained from egg mops laid in the laboratory in aerated synthetic sea water (Instant Ocean brand) during November 1978 by wild-caught adults from the northern Gulf of Mexico. All hatchlings were reared exclusively on a diet of copepods, including *Labidocera aestiva, Acartia tonsa* and other small unidentified species caught in the bay and adjacent waters of Galveston Island. The squids were fed once or twice daily, depending upon food availability and density in the culture tank. The collected copepods were graded into three different size groups (900-571 μm; 570-334 μm; 333-224 μm) by straining them through sieves of plankton netting.

After several false starts, three successful experiments were conducted in which hatchlings survived a maximum of 16, 29 and 40 days, respectively. In the first two experiments, each group of hatchlings was reared in a 66 l rectangular glass aquarium placed within a circular 1500 l water-conditioning tank filled with synthetic sea water. The culture water was circulated by air-lifts. Temperature ranged from 17-22°C, salinity from 32-34 ppt, and pH from 8.2-8.3. Experiment 1 began with 190 hatchlings. Food particle size was increased parallel with hatchling growth. Food densities varied from 0.040 to 0.120 copepods per ml. Approximately 98% of the hatchlings died during the first four days. Of the three hatchlings alive on day 5, one was living on day 7 and it survived until day 16 and attained a length of 2.0 mm ML. In Experiment 2, 125 hatchlings were placed in the aquarium. Food densities ranged from 0.001 to 0.110 per ml. Approximately 95% of the hatchlings were dead by day 5. One hatchling was alive on day 20 and it died on day 29; mantle length was 3.3 mm. In the third experiment, we used a tank system with recirculating natural sea water similar to the one we described for rearing *Loligo opalescens* (Hanlon et al., 1979). Differences were that the size of the rearing tank was increased from 66 l to 93 l, sea water was continually passed through a UV light filter and no sea water was replenished throughout the experiment. Temperature was kept between 16°C and 18°C, salinity from 37-39 ppt, and pH remained near 8.3. The experiment began with 202 hatchlings. Food densities ranged from 0.001 to 0.190 per ml. Ninety-four percent mortality occurred within six days. By day 19, five hatchlings remained. At day 25, one hatchling was alive and it lived until day 40. It had attained a mantle length of 3.1 mm.

In all of our rearing attempts with hatchlings of *Loligo pealei*, at least 95% were dead three to five days after hatching. This time interval coincided with depletion of the internal yolk. Consequently, starvation was the prime cause of death, but the reasons are several. Starvation could result from the improper size, type, and density of food material. The lack of ability to capture live food in the post-yolk-sac stage probably adds to the high early mortality. We have observed a wide disparity in the ability of older hatchlings to maneuver deftly and aggressively to capture prey organisms. Trapping on the water surface due to surface tension is another cause of mortality that occurs immediately after hatching. This problem was partially alleviated by altering the direction of inflow and increasing flow rate to produce surface agitation. Fin damage was noted in hatchlings trapped on the surface, and in others fin damage resulted from contact with the walls of the rearing tank. In squids of any age, fin damage impairs swimming ability and prey capture (Hulet et al., 1979).

The fact that the mantle more than doubled in length in two hatchlings that lived a month or more suggests that the copepod diet was nutritionally sufficient. The relative growth observed in these *Loligo pealei* hatchlings is similar to that of *L. opalescens* reared to the same age (Hurley, 1976; Hanlon et al., 1979). These preliminary results represent a significant advance in squid rearing, because this is the first time that squid hatchlings as small as those of *L. pealei* have ever been raised beyond the yolk-sac stage. Hatchlings of *L. opalescens* and *L. vulgaris* have been successfully reared up to three months (Boletzky, 1974, 1980; Hurley, 1976; Hanlon et al., 1979), but they are twice the size of *L. pealei* at the time of hatching. Our selection of copepods as a preferred food for early hatchlings is also supported by analyses of stomach contents of wild-caught *L. pealei*: the smallest squids examined (down to 22 mm ML) fed primarily upon copepods, chaetognaths and other crustaceans (Vovk, 1974; Whitaker, 1978).

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PHAGOCYTOSIS BY AMOEBOCYTES OF *BIOMPHALARIA GLABRATA*: ABSENCE OF OPSONIC FACTOR. – The role of phagocytosis as an integral component of the defense mechanisms initiated by both vertebrates and invertebrates is well established. However, the role of biologically active humoral factors in initiating or enhancing phagocytosis in invertebrate species requires further elucidation. Studies on the phagocytic activity of molluscan amoebocytes (= hemocytes) have strongly suggested that tissue and hemolymph agglutinins may serve as opsonins (Tripp, 1966; Anderson & Good, 1976; Arimoto & Tripp, 1977; Renwrantz & Mohr, 1978), analogous in function to the cytophilic immunoglobulins and the third component of complement (C_3) on the activity of vertebrate phagocytes (Frank et al., 1975). In spite of demonstrated enhancement of phagocytic activity of some molluscan amoebocytes in the presence of hemolymph or agglutinin-containing tissue extracts, direct association between specific biological substances and the surfaces of amoebocytes has not been adequately demonstrated. The possibility that nonspecific physical and chemical factors present in the hemolymph and tissue extracts may, in fact, be partially responsible for previously reported phagocytosis in molluscs must be seriously considered.

The present study is a continuation of our earlier investigations of the *in vitro* phagocytic activity of *Biomphalaria glabrata* amoebocytes (Abdul-Salam & Michelson, 1980a,b). Its main objective was to determine the possible involvement of humoral factor(s) on the phagocytic activity of the amoebocytes, particularly the naturally occurring hemagglutinin known to occur in the hemolymph and albumin gland of this species (Michelson & DuBois, 1977). The techniques employed in evaluating phagocytic activity (the uptake of formalized erythrocytes by amoebocytic monolayers) are those described previously by Abdul-Salam & Michelson (1980a).

Four separate experiments, each replicated at least three times, were designed to investigate the influence of soluble factors in hemolymph and albumin gland extracts, as well as factors that may be bound to the surfaces of amoebocytes on the uptake of formalized erythrocytes. The results of these studies are summarized as follows.

1. Effect of hemolymph. The uptake of formalized sheep erythrocytes (FSE) was not significantly altered in the presence or absence of homologous hemolymph. However, slight differences in the uptake were observed in monolayers exposed to hemolymph from different strains of the snail.

2. Effect of albumin gland extract. The incorporation of different dilutions of albumin gland extracted in Chernin's balanced salt solution, pH 7.4 (Chernin, 1963), had no significant enhancing effect on uptake of FSE (Fig. 1). However, strong inhibitory effect was observed in the presence of high concentration of the extract. It is possible that the inhibitory effect was due to electrostatic repulsion between amoebocytes and erythrocytes caused by the negatively charged albumin binding the surfaces. Interference by bovine and human albumin and other negatively charged macromolecules upon *in vitro* phagocytosis by vertebrate cells has been indicated by Deierkauf et al. (1977). Further, albumin gland extracts from snails infected for 4 weeks with *Schistosoma mansoni* did not exhibit this inhibitory phenomenon. This, coupled with the report by Christie & Foster (1970) which indicated the depletion of protein in the albumin gland of *Biomphalaria glabrata* parasitized with *S. mansoni*, lends credibility to the thesis that albumin interferes in a negative way with the early steps of amoebocyte-erythrocyte interaction.

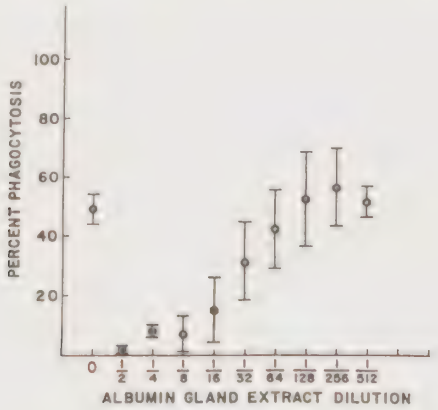

FIG. 1. Phagocytosis of formalized sheep erythrocytes by amoebocytes of *Biomphalaria glabrata* in the presence of hemagglutinin-containing albumin gland extract.

3. Effect of sugars. *In vitro* agglutination of type-A of human erythrocytes by agglutinin in the albumin gland extract is inhibited by specific sugars (Table 1). In order to investigate the possibility of the existence of agglutinin bound to the surface of the amoebocyte that may mediate the attachment of

TABLE 1. Hemagglutination inhibition of *Biomphalaria glabrata* agglutinin by various sugars.

Sugar	Hemagglutination
None	+
n-Acetyl-D-galactosamine	+
n-Acetyl-D-glucosamine	–
L-(–)-Fructose	–
D-(+)-Galactose	+
D-(+)-Glucose	+
D-(–)-Levulose	–
D-(+)-Manose	–
L-(+)-Rhaminose	+
D-(–)-Ribose	+
D-(–)-Sorbitol	+
L-(–)-Sorbose	–
Sucrose	+
D-(+)-Xylose	+

+ = agglutination of type-A of human erythrocytes by albumin gland extract.

– = no agglutination.

erythrocytes, monolayers were exposed to FSE in the presence of sugars that are known to interact with agglutinin and those that do not. The result of this experiment indicated that the uptake of FSF was not significantly altered in the presence or absence of the various sugars.

4. Uptake of type-A and type-O of human erythrocytes. The hemagglutination activity of *Biomphalaria glabrata* agglutinin is directed against only type-A of human erythrocytes. However, we were unable to demonstrate a preferential uptake between types A and O of the erythrocytes.

The results from these studies indicate that *in vitro* uptake of formalized erythrocytes by amoebocytes of *Biomphalaria glabrata* is independent of soluble humoral factors in the hemolymph or in albumin gland extracts, or of factors adherent to the surface of amoebocytes. Nevertheless, this is not indicative of the absence of recognition in the cellular defense system. On the contrary, studies by Tripp (1961) have demonstrated clearly the ability of *B. glabrata* amoebocytes to distinguish between "self" and "nonself" materials by accepting homologous and rejecting heterologous implants. Also, the fact that miracidia of only certain strains of *Schistosoma mansoni* develop unharmed within the snail tissues, while others are attacked and destroyed by amoebocytes immediately upon penetration, proves the existence of a recognition mechanism (Basch, 1976). However, the nature of this mechanism is still obscure, and it does not appear to be analogous to those associated with the vertebrate immune system.

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SHELL SPINATION IN *MELONGENA CORONA*: SUBSPECIES CHARACTERISTIC OR SIZE RELATED? – In their review of the Melongenidae, Clench & Turner (1956) recognized several subspecies of *Melongena corona* Gmelin. Their new subspecies, *M. c. johnstonei*, possessed a single row of spines on the body whorl shoulder, and "rarely" possessed spines near the base of the shell. It was supposedly distributed from northern Florida to eastern Alabama. The typical form, *M. c. corona*, "usually" had a single row of spines at the whorl shoulder and another row at the base of the whorl. These authors stated (1956: 175) that *M. c. corona* was distributed from Keaton's Beach, Taylor County, Florida, south to the north end of Cape Sable, Florida, but stated elsewhere (1956: 179) that it was also found in Apalachee Bay, Florida, where it supposedly merged with *M. c. johnstonei*. In summary, Clench & Turner recognized two subspecies of *M. corona* along the Florida Gulf coast (*M. c. corona* and *M. c. johnstonei*), with the primary distinguishing character being the presence or absence of spines near the base (siphon end) of the shell.

While studying the movements and other behavior of *Melongena corona* in the Apalachee Bay area in 1973, many spined and unspined specimens were encountered. Initial observations suggested that possession of siphonal spines was related to size.

Levy (1979) recently concluded that possession of siphonal spines (basal spines) is related to size in *Melongena corona*, but included no supporting data. Also, Levy statistically compared the relationship between spination frequency and geographic location *separately* from the relationship between spination frequency and snail size. This analytical procedure was improper, because it is not sensitive to possible differences in the size-frequency distributions of snails among the different locations. For example, using Levy's method of analysis, real differences in spination frequency among geographic locations could 'produce' apparent differences in spination frequency relative to snail size, if the size-frequency distributions of snails in the separate samples were different. Levy also failed to include any data on the size of snails in her samples.

The relationship between siphonal spination and size in *Melongena corona* can be demonstrated easier and more clearly by examining one or two popualtions in detail, rather than many populations superficially. Such data are given below.

Methods. A total of 568 *Melongena corona* were examined from barrier beach intertidal zones and oyster bars located along the north and northwest shorelines of Goose Creek Bay, a low energy habitat broadly connected to Apalachee Bay in Wakulla County, Florida. All sites were less than 2 km from one another and separated by water less than 2 m deep at mean sea level. Snails were not selected randomly with respect to size so that size classes could be represented more equally; however, snails were selected randomly with respect to spination. All 42 copulating pairs (84 snails) encountered were examined. Copulation was identified by the stereotyped position of the two snails (described in Hathaway & Woodburn, 1961: 54) and by insertion of the penis of the snail on the right into the mantle cavity of the snail on the left, which lacked a penis.

A total of 175 *Melongena corona* were also examined from low energy intertidal zones along the northeast shoreline of Placida Harbor, Charlotte County, Florida. Finally, 13 *M. corona* were examined from Keaton's Beach, Taylor County, Florida. At the latter two sites, all snails encountered were examined and none were copulating.

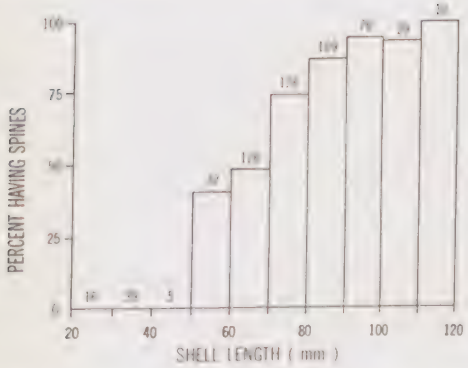
The shell lengths of all snails were measured to the nearest .1 mm with vernier calipers, and the spine configuation was noted. Sex was determined only for copulating pairs. Data on the members of each copulating pair were assigned a pair-specific code number to permit subsequent examination of any relationship between mate selection and spine configuation. Individually numbered plastic tags, file marks on the shell and other procedures insured that no snail was examined more than once.

Results. All *Melongena corona* examined from all three locations possessed a single row of spines around the body whorl shoulder. Of the 568 snails examined from Goose Creek Bay, 372 possessed at least one distinct spine on the dorsal side of the shell near the siphon (this location is equivalent to Clench & Turner's "base of the shell"); 196 snails lacked spines in this location. As Fig 1 reveals, shell length was related to the presence of spines near the siphon in this sample. The smallest snail possessing these spines was 55.7 mm, while the largest snail lacking spines was 106.7 mm. Among intermediate size snails, there was a positive relationship between shell length and the probability of siphonal spines being present.

In Placida Harbor, a location where only *Melongena corona* possessing siphonal spines supposedly occur, 132 of the 175 snails examined lacked siphonal spines. The relationship between size and the proportion of individuals in a size class possessing spines in this sample (Fig. 2) was basically similar to that found in Goose Creek Bay. The smallest snail possessing siphonal spines was 34.1 mm and the largest snail lacking spines was 83.6 mm. Large snails were poorly represented in the Placida sample, probably due to heavy collection by tourists.

Of the 13 *Melongena corona* examined from Keaton's Beach, another location where only snails possessing siphonal spines supposedly occur, only two had siphonal spines; their shell lengths were 51.2 and 57.2 mm. The remaining 11 specimens (mean shell length = 46.2 mm; s.d. = 5.6; range, 33.7 to 56.4 mm) lacked siphonal spines.

It is possible to compute the shell length of 13 snails identified as either *Melongena corona corona* or *M. c. johnstonei* in Clench & Turner (1956, pls. 100-103, 105). All 11 *M. c. corona* illustrated possess



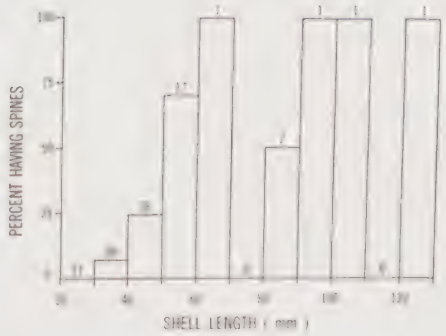


FIG. 1. Size-frequency histogram for 568 *Melongena corona* from Goose Creek Bay possessing at least one spine on the dorsal side of the shell near the siphon. The number of snails in each size class is indicated above each histogram bar. FIG. 2. The same relationship as in Fig. 1 for 175 *M. corona* from Placida Harbor.

siphonal spines and their mean shell length is 74 mm (range, 54 to 105 mm). Both of the *M. c. johnstonei* illustrated lack siphonal spines and their shell lengths are 60 and 105 mm. These data generally fit the relationships between size and possession of siphonal spines shown in Figs. 1 and 2.

For the 42 pairs of snails encountered copulating in Goose Creek Bay, the mean shell length of males was 70.6 mm (s.d. = 8.65; range, 52.1 to 93 mm) and the mean shell length of females was 72.4 mm (s.d. = 12.67; range, 55.7 to 113.3 mm). Table 1 shows the number of pairs of copulating snails observed for each of the four possible combinations of spine configuration, and the number which would be expected if the snails had paired randomly with respect to spination. The absence of a significant difference ($X^2 = .26$, with 3 d.f., $P > .1$) between the observed and expected values indicates that spine configuration and mate selection are unrelated.

TABLE 1. Occurrence of the possible spine configurations for mated pairs of *Melongena corona*.

Spine configuration for mated pairs	Observed occurrence	Expected occurrence
Both spined	14	14.79
Both unspined	6	6.79
Male spined, female unspined	9	8.21
Male unspined, female spined	13	12.21
Total	42	42.00

Discussion. *Melongena corona* with and without siphonal spines occur sympatrically in Goose Creek Bay and interbreed with no evidence that spine configuration influences mate selection (Table 1). Assuming this interbreeding produces offspring having normal reproductive success, there is only one biological species involved.

None of the 64 snails from Goose Creek Bay smaller than 55.7 mm had siphonal spines (Fig. 1). Either all 372 spined individuals in Goose Creek Bay migrated there from *Melongena corona corona* populations (Clench & Turner, 1956) located to the east, after reaching adult size, or siphonal spines are acquired ontogenetically in *M. corona*.

Preliminary data on the movement patterns and capabilities of *Melongena* suggest that the first explanation is unreasonable (unpubl. data). Furthermore, 75.4% of the *M. corona* from Placida Harbor lacked siphonal spines as did 84.6% of the snails from Keaton's Beach. All snails at both of these locations should possess siphonal spines according to Clench & Turner (1956). These data suggest that approximately the

same relationship between size and the probability of possessing siphonal spines exists at all three study sites.

The gradual acquisition of major shell ornaments with growth was also documented for *Ceratostoma foliatum* by Spight & Lyons (1974). In this species, some individuals reached 80 mm in shell length before the first varix developed, although possession of three varices was considered a generic characteristic.

It is concluded that the siphonal spines of *Melongena corona* are acquired ontogenetically and, consequently, that the possession of siphonal spines is not a valid morphological character on which to base a subspecies distinction in this species. Recognition of the distinct subspecies *M. c. corona* and *M. c. johnstonei* is not warranted, since Clench & Turner's (1956) distinction is based primarily on the presence of siphonal spines.

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QUANTIFIABLE ARTIFICIAL RATIONS FOR MOLLUSCAN GRAZING EXPERIMENTS. – In attempts at complete actuarial bioenergetics for molluscan species (see Russell-Hunter, 1978), assessments of respired assimilation, tissue growth and reproductive output for these "balance sheets" are often more accurately based than are corresponding estimates of food intake. Some of the better quantitative studies of ingestion have been on filter-feeding species (Kirby-Smith & Barber, 1974; Newell et al., 1977; Widdows, 1978). Accurate assessment of intake in molluscs grazing on *Aufwuchs* or on macrophytes has proved more difficult, despite a number of studies relating quality of ingested *Aufwuchs* to such parameters as growth and fecundity in snails (McMahon et al., 1974; Hunter, 1975; McMahon, 1975). Our recent studies on the metabolic background of reproductive effort in *Bithynia tentaculata* (Linnaeus) (Tashiro, 1980) and in *Leptoxis (Mudalia, = Spirodon)* (Aldridge, 1980) required the preparation and administration of quantifiable artificial food to experimental groups of these snails. Although based on earlier artificial foods, our new technique of preparation and quantitative use is relatively simple and may prove valuable to other workers.

Among earlier methods of preparation of artificial foods was the production of gel sheets of nominally uniform thickness by "doctor blade" techniques (Standen, 1951; Moore et al., 1953; Hunter, 1975). Similar food sheets have long been used for successful maintenance of cultures of vector snails such as *Biomphalaria* (=*Australorbis*) *glabrata* (Say), but are difficult to quantify. All such foods utilize the gelling of solutions of sodium alginate by calcium chloride, and our recipes (see Table 1) differed from the earlier (British) ones only by substituting brewer's yeast for the dietary supplement preparation *Bemax*, and in the use of sodium caseinate to provide higher protein per milligram dry weight of food. Preliminary studies followed the techniques of the earlier workers: spreading the aqueous slurry on a flat surface with a doctor blade, pouring calcium chloride solution over the sheet, and subsequently cutting discs (using cork-borers) from the gelled layer. Attempts were also made to mold discs. Neither method proved satisfactory for the production of large numbers of uniform food discs for experimental purposes. In fact, punched discs could vary up to 30% in dry weight and more in trophic value (assessed as total organic carbon or as total combined nitrogen).

The new technique which was developed employs a Pasteur pipette to drop (passively) a series of aliquots of slurry onto a sheet of glass which has previously been coated with a thin layer of Mayer's albumin. It is important that the pipette be held at the same angle to the glass sheet during the dispensing of each entire series. Four recipes used for slurries are set out in Table 1, and large batches (made from the same initial supply of ingredients) were made at one time to cover the duration of each set of experiments. The drops of slurry were gelled into discs by adding drops of 2% (by weight) calcium chloride solution. Within experimental sets, the discs produced in this way were very uniform in surface area (maximum variation of 0.5%) and proved to be nearly identical in dry weight (all within a range of 1.4% of mean batch weight). As noted below, subsequent analyses of total organic carbon and of total combined nitrogen content confirmed the nutritional uniformity of the food discs. In experimental use, to allow for correction for any loss by leaching of constitutents during feeding, control discs from the same batch were also placed in water during each feeding period. In fact, over periods of 24 hr submergence, little such leaching was detected.

The four recipes of Table 1 represent high and low protein content, and high and low ash content, and the results of subsequent analyses of control discs from batches of these four artificial foods are set out in Table 2. For these four foods, dry weights of batches of randomly chosen discs (after 24 hrs of leaching) did not vary greatly. Expressed as percentages of the mean values for each batch, standard deviations

TABLE 1. Recipes for slurries for artificial food discs.

Ingredients	Food type			
	High protein/ low ash	Low protein/ low ash	High protein/ high ash	Low protein/ high ash
Sodium alginate	0.1 g	0.1 g	0.1 g	0.1 g
Dried, powdered lettuce	0.1 g	0.1 g	0.1 g	0.1 g
Sodium caseinate	0.05 g	0	0.05 g	0
Brewer's yeast	0.1 g	0.1 g	0.1 g	0.1 g
Calcined infusorial earth	0	0	0.32 g	0.27 g
Water	10 ml	10 ml	10 ml	10 ml

TABLE 2. Analyses of nutrient content of artificial food discs after "control" exposure.

Food type	Per mg food				C:N	µg C per mg food	
	µg C	(s.d.)	µg N	(s.d.)		protein	nonprotein
High protein/high ash	178.5	(10.1)	20.2	(1.8)	8.8	65.7	112.8
High protein/low ash	375.7	(14.3)	42.4	(3.1)	8.8	137.9	237.9
Low protein/high ash	173.7	(8.6)	11.7	(1.4)	14.8	38.1	135.6
Low protein/low ash	349.2	(13.1)	23.5	(2.2)	14.8	76.5	272.7

ranged from 0.48% to 1.27%, averaging 0.84%. As can be seen from Table 2, subsequent analyses showed that variation in total organic carbon (determined by the "wet-oxidation" method of Russell-Hunter et al., 1968) or in total combined nitrogen (determined using a Coleman Model 26 Nitrogen Analyser in a micro-Dumas method of Gustin, 1960) expressed per mg of food is somewhat greater and may even occasionally exceed 4%. In general, however, these food discs provide a more quantitative basis for artificial rations than had previously been available.

The food discs were taken avidly by snails and did not appear to evoke any short-term or long-term adverse effects. Trial groups of snails from the *Bithynia tentaculata* population in Oneida Lake were successfully maintained for eight months on both low protein/low ash and high protein/low ash (see Table 1) versions of the food discs. These trial animals included females which matured and laid eggs yielding viable offspring, and there was no mortality in the eight-month groups.

In the course of this work on the metabolic background of reproductive effort, a new approach has also been made to the even more difficult problem of quantifying ingestion of natural *Aufwuchs* by snails. As in earlier investigations in our laboratory, *Aufwuchs* food was grown on precleaned 2.54 x 7.62 cm microscope slides, initially in submerged racks in the field, where they were held for two weeks. The slides, cleaned on one side, were transferred to trays of appropriate lake or stream water in the laboratory, where they were maintained under fluorescent illumination at Light:Dark = 14:10 hrs and 22°C until used in feeding experiments. Earlier work from this laboratory (Hunter, 1975) utilized such slides (prescored by diamond to break into equal halves), using one half for the experiment and the other for a control. Variation between halves limits this procedure to experiments where grazing is extensive (or amounts to nearly total clearance), while low (but still visible) amounts of snail grazing can result in zero or negative values for ingestion after drying and weighing.

Our new technique is based on the somewhat surprising fact that suitable *Aufwuchs* can be air-dried (at 23°C), then weighed, then rehydrated, again be air-dried and then return to the same "live dry" weight. It uses 2.54 x 2.54 cm "plates" cut from the farmed microscope slides. Before experimental feeding, these plates are blotted free of excess water and then allowed to air-dry to constant weight (four hours at 23°C). After recording the weights, the plates with *Aufwuchs* are rehydrated and fed to snails. After the feeding period, plates are recovered, again blotted and air-dried for four hours. Each weight difference is used as a measure of the amount grazed and can be converted to a true dry weight (constant dry weight in a drying oven set at 80-85°C). Control plates taken through this sequence of treatments do not lose any measureable weight of *Aufwuchs*. Measures of weight ingested by this method correspond more closely to estimates of percentage area grazed than do those from any other weighing technique.

The usual protocols for our feeding experiments with food discs (or with *Aufwuchs* plates) are based on previous estimates of gut clearance times for each species, and involve a period for emptying the gut followed by a similar period of pre-experimental feeding on the specific diet. After removal of all faeces and uneaten food discs, the experimental ration of food is provided and the animals monitored through the experimental period. At the end of the feeding period, discs and parts of discs remaining uneaten are removed, dried and weighed (along with the control food discs and also collected and counted faecal pellets). Combined samples of faecal pellets (along with control food discs) are later analysed for total organic carbon and total combined nitrogen. Tissue dry weights are determined for the experimental snails after fixation and decalcification. From these various data, we can compute weight-specific rates of ingestion and of assimilation for proteinaceous and nonproteinaceous food under various experimental conditions.

Food discs prepared by the above technique have now been successfully used to assess food intake for a series of experiments on metabolic turnover in *Bithynia tentaculata* (Tashiro, 1980) and in *Leptoxis (Mudalia, = Spirodon) carinata* (Bruguière) (Aldridge, 1980). It is hoped to publish elsewhere full accounts of concurrent assessments of oxygen consumption and nitrogenous excretion in relation to food intake and reproductive effort in these two species.

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MYTILOPSIS SALLEI (RECLUZ) (BIVALVIA: DREISSENACEA) RECORDED FROM HONG KONG: AN INTRODUCTION BY VIETNAMESE REFUGEES? – The Central American dreissenid *Mytilopsis sallei* (Recluz) (Marelli & Berrend, 1978) was introduced into Visakhapatnam harbour, on the east coast of India, sometime around 1967 (Ganapati et al., 1971). The precise route of this invasion is unknown. *M. allyneana*, recorded only from Fiji by Hertlein & Hanna (1949), and *M. africana*, from the west coast of Africa (Morton, 1970), are possibly both synonymous (Morton, 1980), indicating that the spread of *M. sallei* was either from the east, via the Panama Canal (opened in 1915), or from the west, across the Atlantic Ocean. As noted by Morton (1980), the precise taxonomic status of *M. sallei* is unknown. Only two facts are certain: a species called *M. sallei* has been introduced into Visakhapatnam harbour and there have been no subsequent reports of it outside this location (other than in its natural range).

On 22 April 1980, during participation in the First International Workshop on the Marine Flora and Fauna of Hong Kong and Southern China, held at Wu Kwai Sha, Tolo harbour, New Territories, Hong Kong, from 19 April to 8 May, a large piece of driftwood stranded on the beach near the pier at Wu Kwai Sha (Fig. 1) was examined. The driftwood was judged to be planking from a wooden vessel and was covered on the outside (but *not* the inside) by *Balanus amphitrite amphitrite* (Darwin) and by a dense cover of *Mytilopsis sallei* (Fig. 2). No other foulers, particularly pelagic species, were found.

A sample of the dead bivalves was collected and each specimen was measured along its greatest length to the nearest 1 mm. An earlier study (Morton, 1980) of *Mytilopsis* in Visakhapatnam has established the population structure for this species at that location and shown it to be a very rapid growing, fast maturing opportunist. The length-frequency histogram obtained from the sample of *M. sallei* from Hong Kong has been overlaid here on the histogram of the Visakhapatnam sample (Fig. 3). Morton (1980) showed that the Visakhapatnam sample comprised two major peaks which, he speculated (in the absence of any long-term studies on the population dynamics of this species), represented two spatfalls occurring respectively in April and June 1975. The single population peak of the Hong Kong sample would thus, if any analogy is allowed, be equivalent to the April spatfall of the Visakhapatnam population. According to the growth rate studies of Mangapathi Rao et al. (1975), these specimens, ranging in length between 3-18 mm and comprising a single peak, would have attained this size in approximately one month or less.

It seems distinctly improbable that a wooden-hulled vessel, presumably on a legitimate voyage, would sail or motor from Visakhapatnam around the Straits of Singapore and be wrecked on Hong Kong's coasts

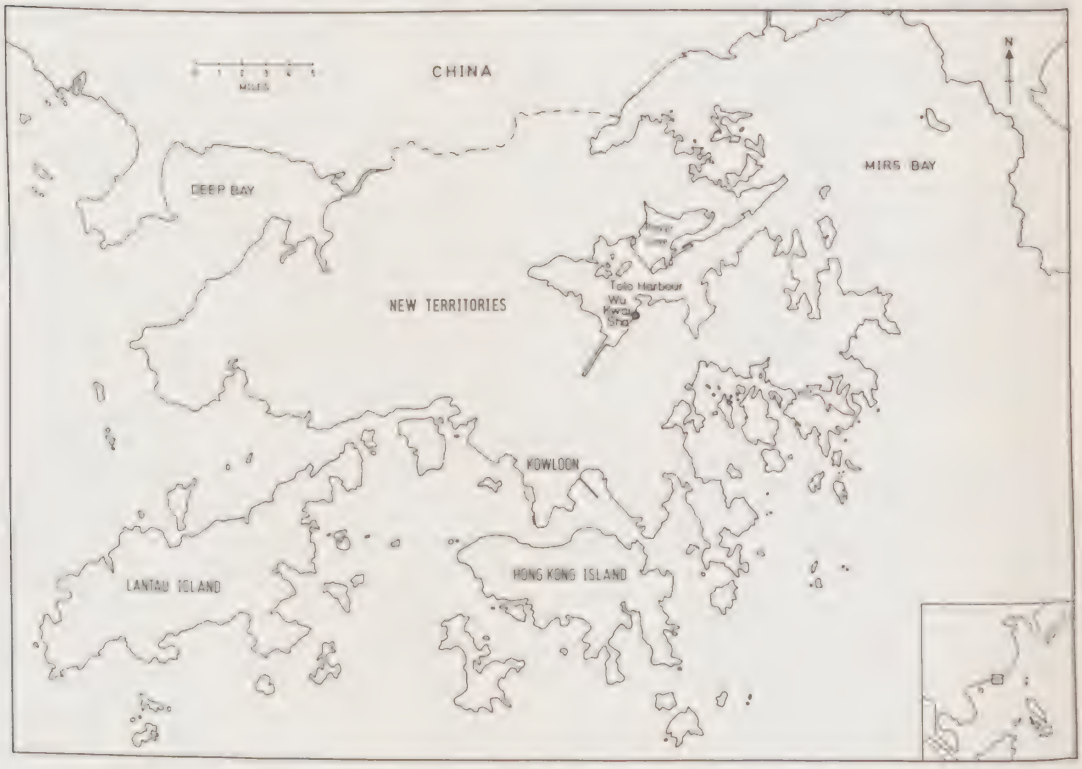

FIG. 1. A map of Hong Kong showing the location of Wu Kwai Sha in Tolo harbour.

FIG. 2. *Mytilopsis sallei*. A, From Visakhapatnam harbour, India; B, from driftwood in Hong Kong.

with no report being made. The absence of any pelagic foulers supports this view. There are, however, small, wooden-hulled vessels arriving in Hong Kong in large numbers, from two major sources: first, refugees from Vietnam and, second, illegal immigrants from the People's Republic of China. Most arrive directly from Vietnam in the case of the former (though they apparently may stop in Chinese ports or at Macau) or from other parts of the Chinese coast in the case of the latter. When they arrive in Hong Kong, and if they avoid detection, their boats are usually found beached. If apprehended, their boats are often dynamited at sea by the Hong Kong authorities.

Both *Mytilopsis sallei* and *Balanus amphitrite amphitrite* are harbour species, and there can be little doubt that these foulers were picked up by a small wooden-hulled vessel in a port close to Hong Kong, either in China or Vietnam. How *M. sallei* originally arrived in the South China Sea is unknown. The species has thus established itself at some unknown location(s) on the coast of the South China Sea. Now, if this floating population was able to release gametes prior to being stranded, it possibly may be also in Hong Kong.

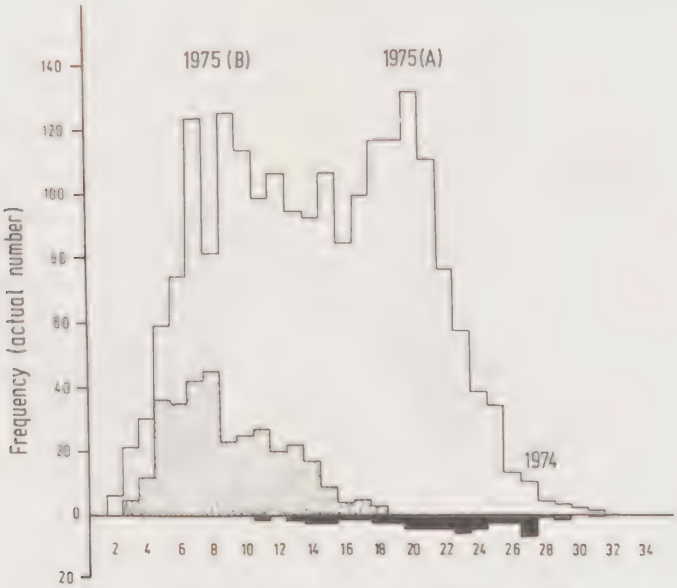

FIG. 3. A length-frequency histogram of the population of *Mytilopsis sallei* colonising the Naval jetty in Visakhapatnam harbour, India, in July 1975 (after Morton, 1980). Overlaid is the population structure of the sample of *M. sallei* from Hong Kong, collected in April 1980.

It seems possible that, in this case, the bivalves have been introduced by refugees, probably from Vietnam. Such a situation was not envisaged by Morton (1980) when he gave a warning against accidental introduction of this species into other parts of the Pacific from Visakhapatnam. *Mytilopsis sallei* is a fouler of great importance, as evidenced by the Visakhapatnam experience (Ganapati et al., 1971; Morton, 1980), but it seems pointless to reiterate earlier warnings against further introductions. Any reports of its occurrence within the Pacific, however, would be invaluable so as to plot and understand the reasons for its spread.

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MISCELLANEA

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BIOGRAPHICAL SKETCH AND MALACOLOGICAL PUBLICATIONS OF MAX MAPES ELLIS, 1887-1953

Nancy E. Brandauer

Max Mapes Ellis, educator and physiologist, was born in Lawrence, Indiana, on December 3, 1887. His father was an educator and President of Vincennes University. He attended the Idaho State Normal School (later to become the Southern Idaho College of Education) and the University of Illinois and received his B.A. (in 1907), M.A. (in 1908) and Ph.D. (in 1911) from Indiana University. In 1910 he served as Director of the Gimbel Scientific Expedition to British Guiana, where he collected gymnotid eels and added a new species, *Porotergus gimbeli*, to the family Gymnotidae; this work later formed a portion of his doctoral thesis. He also did some work early in his career on regeneration in tadpoles.

In 1911 Dr. Ellis was appointed as an Instructor and in 1914 he was promoted to Assistant Professor of Biology at the University of Colorado, continuing in the latter position until 1918. Many of the eels he accumulated during the course of his thesis work remain in the collection of the University of Colorado Museum. While he was at Boulder, he and Professor Junius Henderson collaborated in writing a series of seminal papers on the fishes, Amphibia and Reptilia of Colorado.

The summers from 1913-1917 were spent at the Biological Station of the University of Michigan, where he worked on the taxonomic zoology of various species of worms; in 1919 he described the branchiobdellid worms in the collections of the United States National Museum. In addition, he did extensive collecting of crustaceans, fishes and sponges in Colorado, Indiana, Michigan and New York; these remain in the custody of the University of Colorado Museum.

He joined the faculty of the University of Missouri in 1919 as Assistant Professor of Physiology, becoming Associate Professor in 1923, Professor in 1927 and Chairman of the Department of Physiology and Pharmacology in 1936. During his chairmanship, the Department's professorial staff was tripled, several service courses – including human physiology

Max Mapes Ellis, 1887-1953

for non-science majors and pharmacology for nurses – were developed, and an electrocardiographic service was introduced for the University hospitals and maintained by the Department. In 1930, as a direct result of his labors, the University was designated, in conjunction with the University of California, the University of Michigan and Harvard University, as one of four special laboratories for research work by the U.S. Bureau of Fisheries.

His own research was wide-ranging and included zoology, botany, physiology, physics and chemistry. It also caused him to travel widely. His human physiological research began in 1918 at the Medical Research Laboratory at Hazlehurst Air Field, New York. For several summers, beginning in 1924, he worked at the U.S. Biological Station in Fairport, Iowa, and during a sabbatical in 1927-1928 he did research at the Physiological Institute at the University of Glasgow, Scotland. He directed and carried on an intensive study of streams and impounded waters in the United States, Canada and Mexico, investigating the effects of garbage, silt, poisons and other pollutants on freshwater mussels and game fish.

He was married in 1909 to Marian Lee Durbin, later a co-author of many of his 83 published papers; they had a daughter. His death occurred in Los Angeles on August 26, 1953.

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A PRACTICAL GUIDE

TO THE IDENTIFICATION OF

AFRICAN FRESHWATER SNAILS

DANISH BILHARZIASIS LABORATORY
in collaboration with the
WORLD HEALTH ORGANIZATION

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A PRACTICAL GUIDE TO THE IDENTIFICATION OF AFRICAN FRESHWATER SNAILS

Flemming Frandsen, Fergus McCullough and Henry Madsen

INTRODUCTION

This guide to the identification of African freshwater snails has been prepared with the aim of helping persons engaged in field work, but who have had no specialized training in taxonomy, to assign the snail specimens which they collect to certain groups or taxa by means of a simple identification key. A glossary is given on pp. 117-118.

The guide pays special attention to the principal snail groups which transmit schistosomiasis, such as *Bulinus* and *Biomphalaria*, as well as to *Lymnaea*, which transmits fascioliasis (liver-fluke disease) in cattle, sheep, etc. Thus, in most cases, with the aid of this guide it should be possible to determine whether or not certain specimens are potential snail hosts of human schistosome parasites or are merely snails of no particular medical or veterinary importance. Such knowledge is, of course, essential before implementing rational snail control operations.

The key to the identification of snails begins on p. 100. The procedure is very simple. In each numbered "couplet" (i.e., in each set of two opposing statements), two statements are made, of which only one conforms to the snail to be identified. The correct answer leads either to another numbered set of opposing statements or assigns the snail to a definite family, genus or species. The average size of the adult specimen is shown beside the drawing of the shell.

As a further means of identification, to show shape, size and surface texture or markings, photographs of various pertinent snail species appear at the end of the key. However, it should be stressed that these represent only a small proportion of the approximately 270 species of freshwater snails which have been recorded in waterbodies throughout the African continent.

Should more specific identification be desirable, requiring among other aspects the microscopic examination of anatomical characters, the student is referred to the Field Guides to African Freshwater snails (North East Africa, West Africa, East Africa, South East Africa or Central Africa), published by the Danish Bilharziasis Laboratory in collaboration with the World Health Organization (WHO) (see reference list on p. 119). These guides are freely available on request.

The snails from Lake Tanganyika and Lake Malawi are not included in this guide.

The Danish Bilharziasis Laboratory, in its capacity as WHO Collaborating Centre for Snail Identification, welcomes any opportunity to assist in the identification of freshwater snail specimens, living or preserved, from any part of the world. Notes on the collection, preservation and despatch of snails are given below. Collections should be sent to the following address: Danish Bilharziasis Laboratory, Jaegersborg Alle 1 D, DK-2920 Charlottenlund, Denmark.

We would appeal to readers to send us your comments and criticisms, so that we could take account of them in the preparation of any future edition of this practical guide.

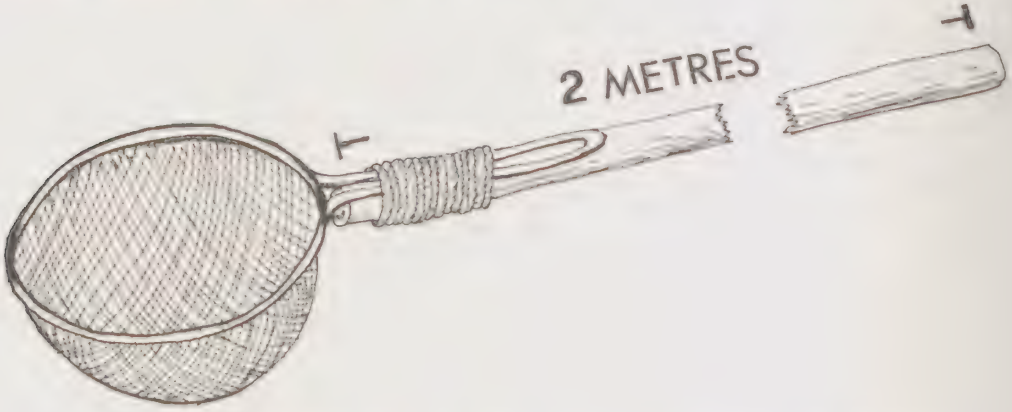
COLLECTION, PRESERVATION, STORAGE AND DESPATCH OF SNAILS

Collection

In schistosomiasis endemic areas, it is not advisable to collect freshwater snails by hand,

because the risk of becoming infected with *Schistosoma* is too great. Rubber or plastic gloves can be used to protect against infection, but they are unpleasant to wear in hot climates. The use of a strong, long-handled scoop is preferable. The net should be shaken in water after it has been through submerged vegetation. Most snails will loosen their hold on the plants and drop to the bottom of the scoop. The contents may then be emptied into a white enamel tray where it is easy to see the snails and pick them up with a pair of forceps.

If the snails are wanted alive, they survive better when transported under cool, damp conditions (see "despatch of living snails", below).



A long-handled kitchen sieve, which can make a useful temporary snail collecting scoop.

Preservation

The simplest way of preserving snails is to put them in 70% ethyl alcohol. The volume of alcohol preferably should be at least twice that of the snails. After some days, the alcohol should be changed because at that time the first volume will have become diluted.

Storage of shells

When snails have been kept in alcohol for some days or killed in boiling water, it is usually possible to extract the body with the aid of a pin bent in the shape of a small hook. It is seldom possible to extract the bodies of small snails, and in such cases the soft parts are allowed to dry inside the shell. After the shells are completely dry, they should be put into suitable tubes and labelled.

Snail Species: L. natalensis
B. truncatus
Locality: Kelagoon, Ghana
Date: 14:03: 1979
Collector: D. Kofi

A typical label, similar to that which should accompany each snail collection.

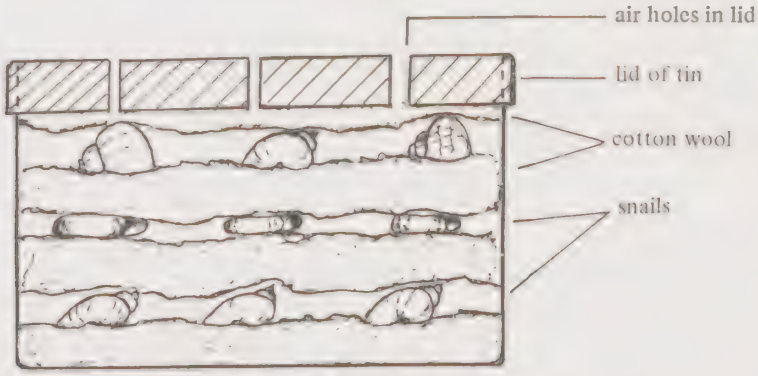
Storage of snails

Preserved specimens are best kept in tightly capped containers. Any evaporation should be prevented and metal caps which rust should be avoided. Each sample, of course, should

be labelled in the same way as the shells.

Despatch of living snails

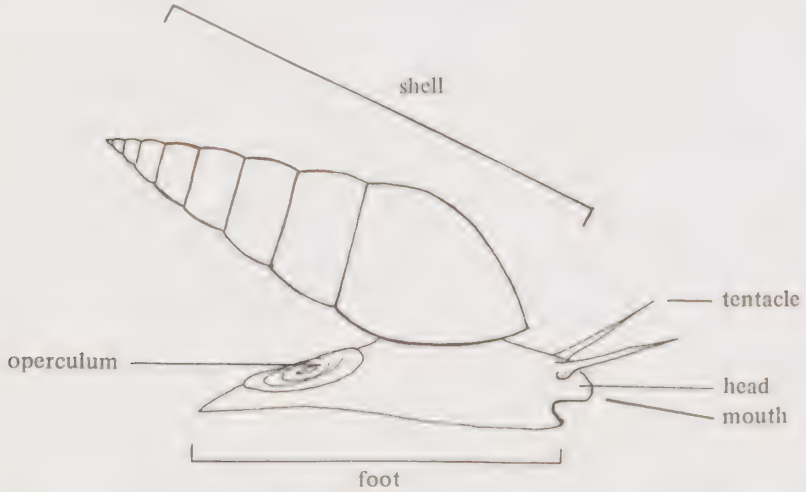
The snails should be sent by airmail. The best way of packing is to place the specimens carefully between layers of damp (not wet) cotton wool in a tin pierced with holes, which will allow ventilation (see figure below). The cotton wool used for layering first should be moistened with pond water and then thoroughly squeezed to get rid of excess water. The specimens should be laid on the cotton wool, allowing a distance between individuals corresponding to the largest shell measurement; thus, if a snail should die during shipment, the putrefaction will not harm the others. Labels for the snails should be placed both inside and outside the tin, as usual, showing locality where found, date, collector's name/address, etc.



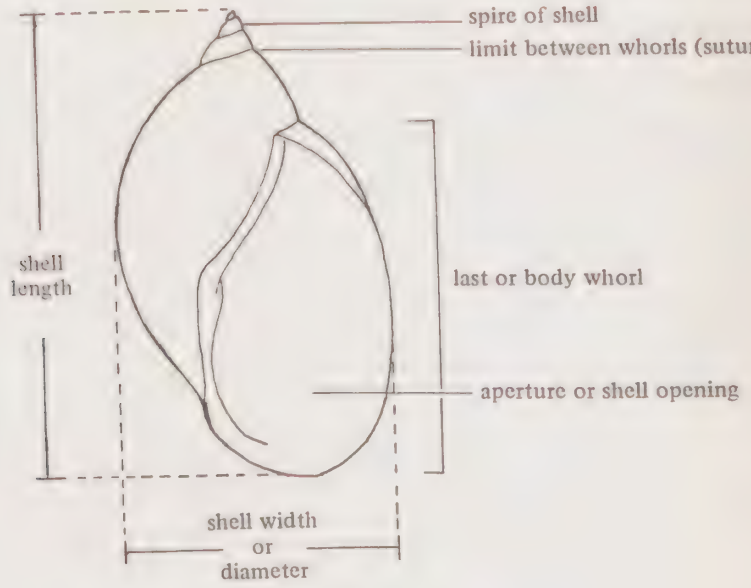
Cross-section sketch of living snails packed in a metal container for air despatch.

SOME EXTERNAL FEATURES OF SNAILS HELPFUL FOR IDENTIFICATION

An understanding of the main characteristics of a typical snail and its shell, as shown below, will be helpful when using the key. In endemic areas, it is preferable to use living snails for identification purposes.



Some features of a snail, showing the parts of its body extended outside its shell.

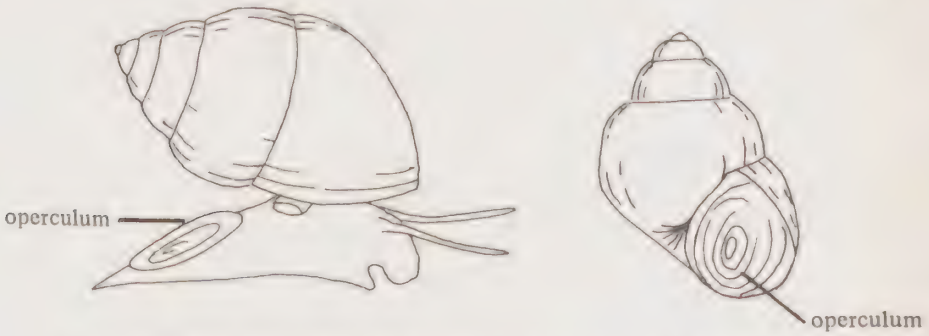


Some features of an empty snail shell.

KEY TO IDENTIFICATION OF AFRICAN FRESHWATER SNAILS OF MEDICAL AND VETERINARY IMPORTANCE

African freshwater snails belong to two main groups, the prosobranchs (Subclass Prosobranchia) and pulmonates (Subclass Pulmonata), which easily can be distinguished as described below.

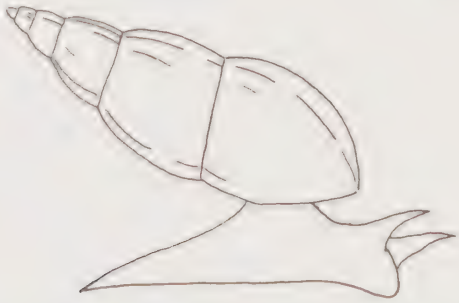
1a Snail with an operculum which blocks the opening of the shell when the body is withdrawn into the shell. Members of this group are **prosobranchs** . . . . . Proceed to couplet 8 (page 108)



[In Africa, several prosobranch families occur, of which only a few species are of any medical importance as intermediate hosts of lung and intestinal flukes. In Africa, these flukes are of minor importance. In Southeast Asia, however, some groups of prosobranchs are involved in the transmission of several trematode diseases of major socio-economic importance.

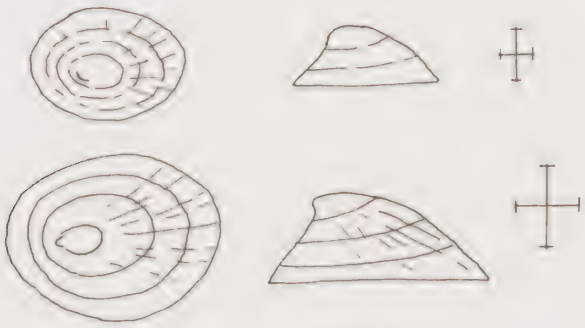
It is possible to assign some of the species to their families by referring to the drawings on pp. 109-110.]

1b Snail without an operculum or lid to cover its shell aperture. All such snails are **pulmonates** . . . . . Proceed to couplet 2, below



[The pulmonates are a very important snail group, since many members are involved in the life cycles of blood, liver and stomach flukes.]

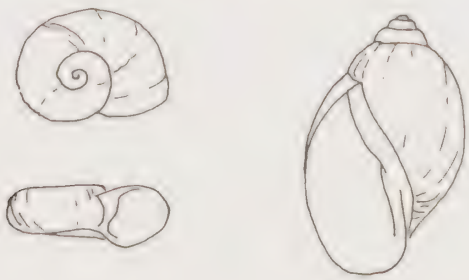
2a Shell cap- or tent-shaped and very small, about 5 mm in length . . . . . Family **Ancylidae**



Top and side views; dimension scales twice natural size.

[In Africa, no member of the ancylid group is of medical importance, but in India a species (*Ferrissia tenuis* (Bourguignat)) belonging to this family is suspected to act as the intermediate host of *Schistosoma haematobium* (Bilharz), which causes urinary schistosomiasis. In Africa, the family Ancylidae contains at least 21 species belonging to the following three genera: *Ancylus, Burnupia* and *Ferrissia*.]

2b Shell spirally coiled, as shown in the figure below . . . . . 3 (page 102)

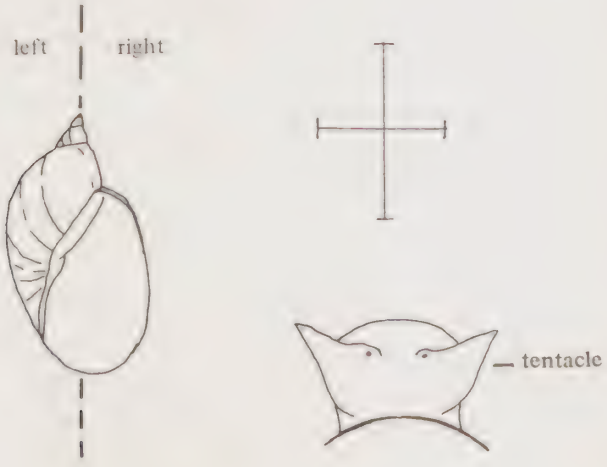


3a Shell higher than wide . . . . . 4, below

3b Shell discoidal, i.e., is coiled in one plane (see drawings below).
Family **Planorbidae** (in part), Subfamily **Planorbinae** . . . . . 6 (page 106)

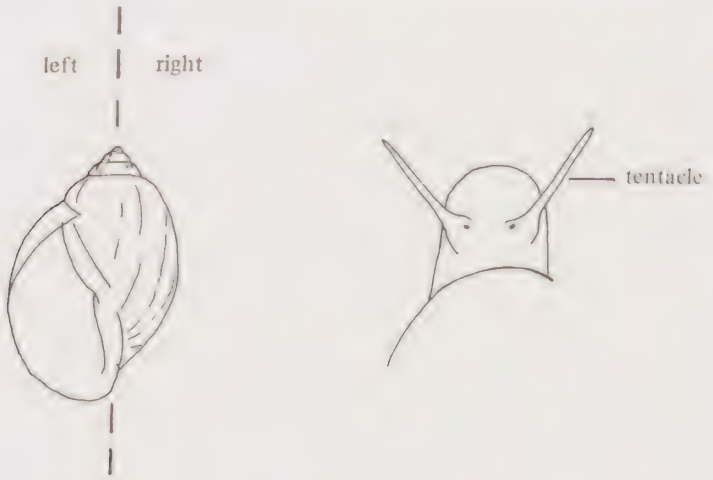
[These snails are members of the family **Planorbidae**, subfamily **Planorbinae**. The latter comprises nine genera in Africa. Many of the species are of great economic importance as transmitters of various fluke diseases. The genus *Planorbarius*, which occurs in Morocco, Algeria and Tunesia, is not included in the key to the Planorbinae (pp. 106-108). The species, *P. metidjensis* (Forbes), is suspected of being the intermediate host for *Schistosoma haematobium* in Portugal and Morocco, but its status as transmitter is still not clearly defined.]

4a Shell opening (aperture) towards the right hand side (see drawing), and tentacles are triangular and flattened . . . . . Family **Lymnaeidae**

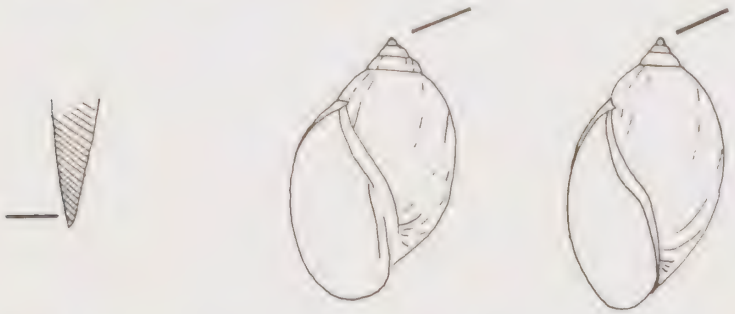


[At least three different species occur in Africa, but only one is common, *Lymnaea (Radix) natalensis* Krauss, which is the intermediate host of the large liver fluke *Fasciola gigantica* (Cobbold), a very common parasite of cattle, sheep and goats, causing much economic loss. Two other species, *L. (Fossaria) truncatula* (Müller) and *L. (Pseudosuccinea) columella* Say, may also act as the intermediate host for species of *Fasciola*.]

4 b Shell opening towards the left hand side (see drawing), and tentacles are slender and tubular in shape . . . . . 5, below

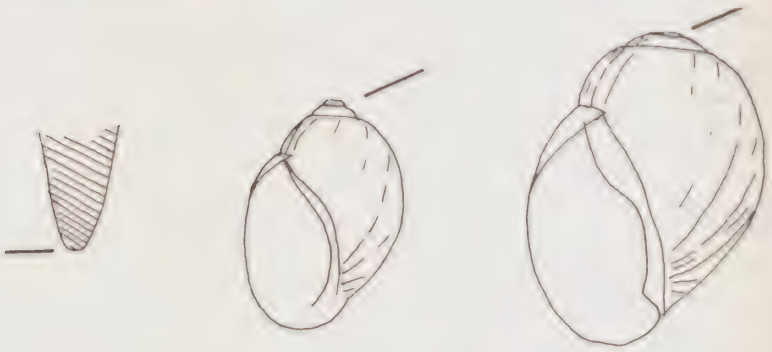


5 a Shell with pointed spire, the sutures between whorls shallow. Living specimens move much faster than snails belonging to couplet 5b. When snail is moving, it is possible to see the very pointed foot (see drawing below). The blood is colourless . . . . . Family **Physidae**



[*Physella* and *Stenophysa* are the genera of this family occurring in Africa. The most common species in Africa is *P. acuta* (Draparnaud), which is of no economic importance. Sometimes it may become infected with bird schistosomes, which can cause "swimmer's itch", a nearly world-wide affliction.]

5 b Shell with blunted spire. Sutures between the whorls appear deeper. In comparison with *Physella*, the members of this group move very slowly and the blood is red . . . . . Subfamily **Bulininae** and genus ***Bulinus***



[**Note.** It sometimes can be difficult to separate *Physella* and *Bulinus* from each other. For further information on the characters of these two genera, see the "Field Guides" mentioned in the reference list on p. 119.]

Many species of the genus *Bulinus* can act as the intermediate hosts of different species of schistosomes, the parasites which cause schistosomiasis. They also may transmit species of a common stomach fluke (family Paramphistomatidae) of cattle.

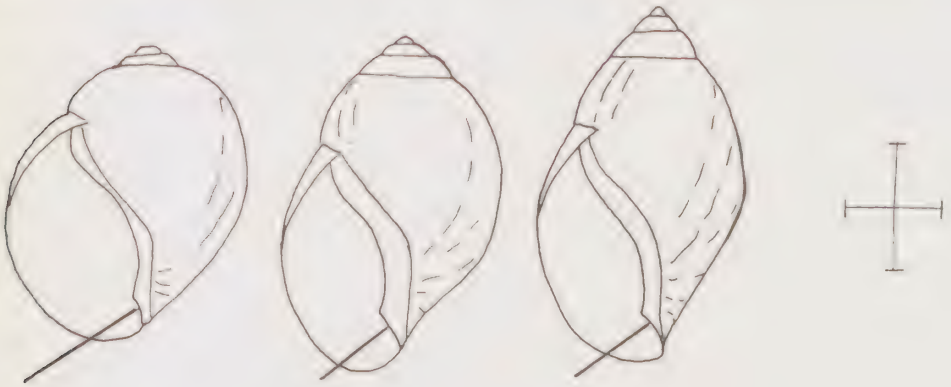
The genus *Bulinus* is divided into four groups according to morphological, anatomical and biochemical differences. A more detailed key for identifying the species is given in the Field Guides (see reference list). A few of the important members of the four groups are described briefly below, but all the species in each group are mentioned. There still is discussion about the number of species, their validity and inter-relationships.

Reticulatus group

The members of this group are very small in size and live in temporary pools. Under laboratory conditions they act as intermediate hosts of *Schistosoma haematobium, S. intercalatum* Fisher, *S. bovis* (Sonsino) and *S. mattheei* Veglia & Le Roux. The *reticulatus* group comprises two species only: *Bulinus reticulatus* Mandahl-Barth and *B. wrighti* Mandahl-Barth. *B. reticulatus* has a scattered distribution from Ethiopia to South Africa.

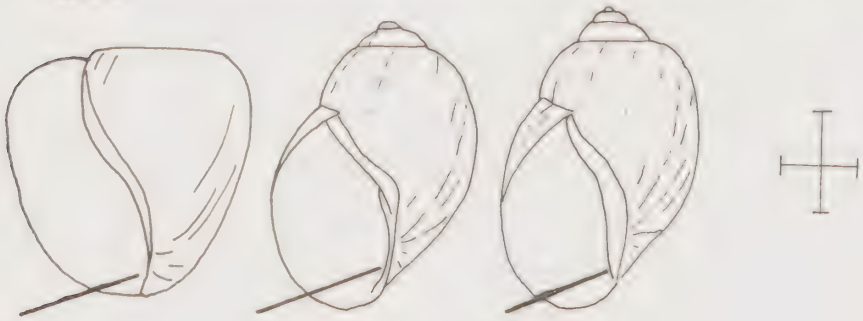
Africanus group

Members of this group are the largest species of *Bulinus*, and they occur all over Africa south of the Sahara. Note the truncation or bend on the inner border of the opening of the shell. The most common and important species is *B. globosus* (Morelet). In East Africa, two other important intermediate hosts occur, *B. africanus* (Krauss) and *B. nasutus* (Martens). Other species in the *africanus* group are *B. abyssinicus* (Martens), *B. hightoni* Brown & Wright, *B. jousseaumei* (Dautzenberg), *B. obtusispira* (Smith), *B. ugandae* Mandahl-Barth and *B. umbilicatus* Mandahl-Barth. The species belonging to the *africanus* group act as the intermediate hosts of *Schistosoma haematobium* and some of the species also transmit *S. intercalatum, S. bovis* and *S. mattheei*.



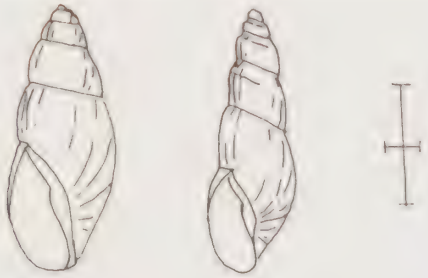
Truncatus/Tropicus group

This group consists of larger species, and the inner border of the shell has no truncation as found in members of the *africanus* group. There are many species in this group, and their identification can be difficult; for further information refer to the "Field Guides" listed in the References. The most important and widely distributed species is *Bulinus truncatus* (Audouin), which acts as intermediate host for *Schistosoma haematobium* and *S. bovis*. Another common species, *B. tropicus* (Krauss), which occurs in the eastern part of Africa, is not a transmitter of human schistosomes but may act as the intermediate host for stomach flukes, as well as for the schistosome *S. margrebowiei* Le Roux in cattle. Other species in the *truncatus/tropicus* group are *B. angolensis* (Morelet), *B. coulboisi* (Bourguignat), *B. depressus* Haas, *B. guernei* (Dautzenberg), *B. hexaploidus* Burch, *B. liratus* (Tristram), *B. natalensis* (Küster), *B. nyassanus* (Smith), *B. octoploidus* Burch, *B. permembranaceus* (Preston), *B. succinoides* (Smith), *B. transversalis* (Martens) and *B. trigonus* Martens.



Forskalii group

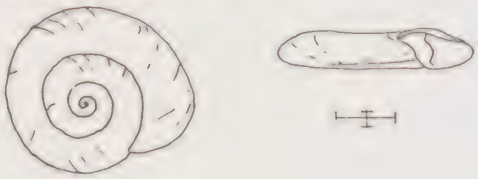
Species constituting this group have shells which are often smaller and more slender than those of the previously mentioned *Bulinus* groups. The most widely distributed species is *B. forskalii* (Ehrenberg). Other species are *B. barthi* Jelnes, *B. bavayi* (Dautzenberg), *B. beccarii* (Paladilhe), *B. browni* Jelnes, *B. camerunensis* Mandahl-Barth, *B. canescens* (Morelet), *B. cernicus* (Morelet), *B. crystallinus* (Morelet), *B. scalaris* (Dunker) and *B. senegalensis* Müller. Some members can act as the intermediate host for *Schistosoma haematobium, S. intercalatum* and *S. bovis.*



6a Small species, with height of shell less than 2 mm . . . . . .
. . . . . See the five genera listed and figured below

[There are five different genera of "small planorbs" in Africa, some being widely distributed. A representative of each genus is shown below. *Ceratophallus* acts as intermediate host for some species of the family Paramphistomatidae.]

Ceratophallus (at least nine species)



Gyraulus (at least two species)

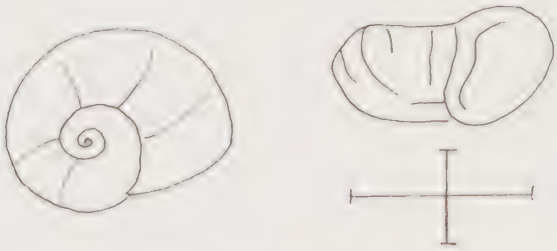
Afrogyrus (at least two species)

Lentorbis (at least four species)

Segmentorbis (at least three species)

6 b Large species, height of shell being more than 3 mm . . . . . 7, below

7 a Shell up to 14 mm in height . . . . . Genus *Planorbella*



[Only one species occurs in Africa, *Planorbella duryi* (Wetherby). This species was formerly placed in the genus *Helisoma*. It is an American species recently introduced into Africa either accidentally or for experimental biological control purposes, in which it possibly may prove useful. *P. duryi* cannot act as intermediate host for flukes of importance. In Africa, it has been reported to occur in 10 different countries, but confirmation of its current distribution is needed.]

7 b Shell less than 6 mm in height . . . . . Genus *Biomphalaria*

Snails of this genus may act as intermediate hosts of *Schistosoma mansoni* Sambon and also of some paramphistome flukes. The genus *Biomphalaria* is divided according to certain shell characters into four groups. A detailed key and description is given in the "Field Guides". An important species for each of the groups is shown below, and all members of the groups are mentioned.

Sudanica group

Biomphalaria sudanica is common in East Africa, where it can be an important intermediate host. The *sudanica* group comprises the following species: *B. sudanica* (three well-separated subspecies, *B. s. sudanica* (Martens), *B. s. tanganyicensis* (Smith) and *B. s. rugosa* Mandahl-Barth, are recognized), *B. camerunensis* (composed of two subspecies: *B. c. camerunensis* (Boettger) and *B. c. wansoni* Mandahl-Barth).

Pfeifferi group

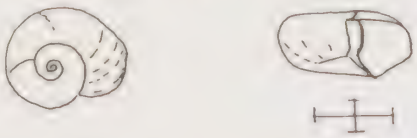
Shell with few very rapidly increasing whorls. This is the most widely distributed group of *Biomphalaria* in Africa. The most common species is *B. pfeifferi* (Krauss), which is also the main intermediate host for *Schistosoma mansoni* (which causes intestinal schistosomiasis) in Africa. The other species belonging to this group include *B. salinarum* (Morelet) and *B. rhodesiensis* Mandahl-Barth).

Alexandrina group

The most important species in this group is *Biomphalaria alexandrina* (Ehrenberg), occurring only in the Nile Valley, where it is the transmitter of *Schistosoma mansoni*. The other species belonging to this group is *B. angulosa* Mandahl-Barth.

Choanomphala group

These are relatively small species with high whorls. They are found almost exclusively in some of the greater lakes in East Africa. The most important species is *Biomphalaria choanomphala* (Martens) from Lake Victoria, where it acts as intermediate host of *Schistosoma mansoni*. Other species belonging to this group are *B. smithi* Preston and *B. stanleyi* (Smith).



8 **Prosobranchia.** The following drawings illustrate some common families of prosobranch snails in Africa. (*All of the snails belonging to this group have an operculum.*)

Neritinidae

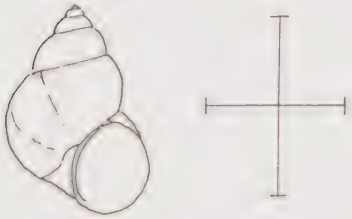
The family Neritinidae in Africa contains the following three genera: *Neritina* (with nine species), *Neritilia* (one species) and *Theodoxus* (one species.

Neritina glabrata Sowerby

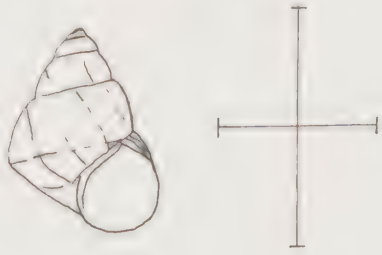
Theodoxus niloticus (Reeve)

Viviparidae

The family Viviparidae in Africa contains only one genus, *Bellamya*, with 17 species.



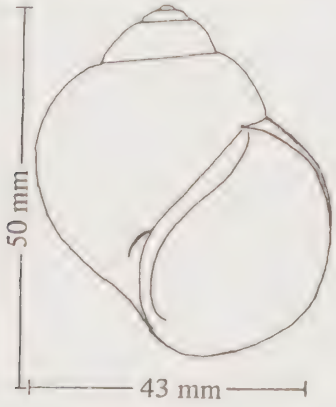
Bellamya unicolor (Olivier)



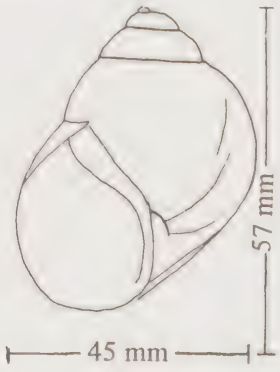
Bellamya capillata (Frauenfeld)

Ampullariidae

The Ampullariidae in Africa contains four genera: *Lanistes* (18 species), *Pila* (four species), *Saulea* (one species) and *Afropomus* (one species).



Pila ovata (Olivier)



Lanistes ovum Peters

Bithyniidae

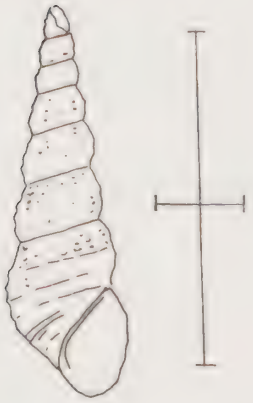
The family Bithyniidae in Africa contains eight genera: *Gabbiella* (22 species), *Jubaia* (two species), *Limnitesta* (one species), *Congodoma* (one species), *Funduella* (one species), *Incertihydrobia* (one species), *Serraia* (one species) and *Soapitia* (one species).

Gabbiella sp.

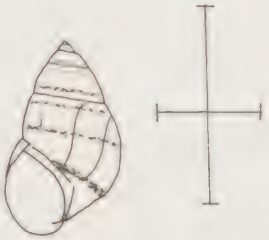
Gabbiella sp.

Thiaridae

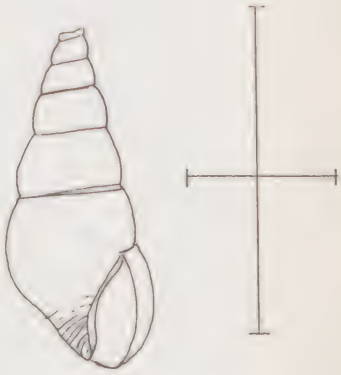
The family Thiaridae contains seven genera: *Melanoides* (28 species), *Potadoma* (17 species), *Cleopatra* (15 species), *Potadomoides* (four species), *Pseudocleopatra* (four species), *Pachymelania* (three species) and *Thiara* (two species). In West Africa, *Potadoma freethi* (Gray) acts as the first intermediate host for the lung fluke *Paragonimus* sp.; the second intermediate host is a crab.



Melanoides tuberculata (Müller)



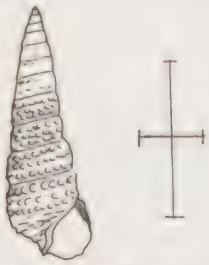
Cleopatra ferruginea (I. & H.C. Lea)



Potadoma freethi (Gray)

Potamididae

The family Potamididae contains one genus with one species. *Pirenella conica* (Blainville) lives in brackish water; it can act as intermediate host for *Heterophyes* sp., a common intestinal parasite found in humans in Egypt; the second intermediate host is a fish.



Pirenella conica (Blainville)

Potadoma freethi

Lymnaea natalensis

Physa acuta and *P. marmorata*

Gyraulus costulatus

Afrogyrus coretus

Ceratophallus natalensis

Biomphalaria pfeifferi

Biomphalaria sudanica

Biomphalaria alexandrina

Distribution maps for some freshwater snails of medical or veterinary importance in Africa.

Biomphalaria camerunensis

Biomphalaria angulosa

Biomphalaria choanomphala

Bulinus reticulatus

Bulinus africanus

Bulinus globosus

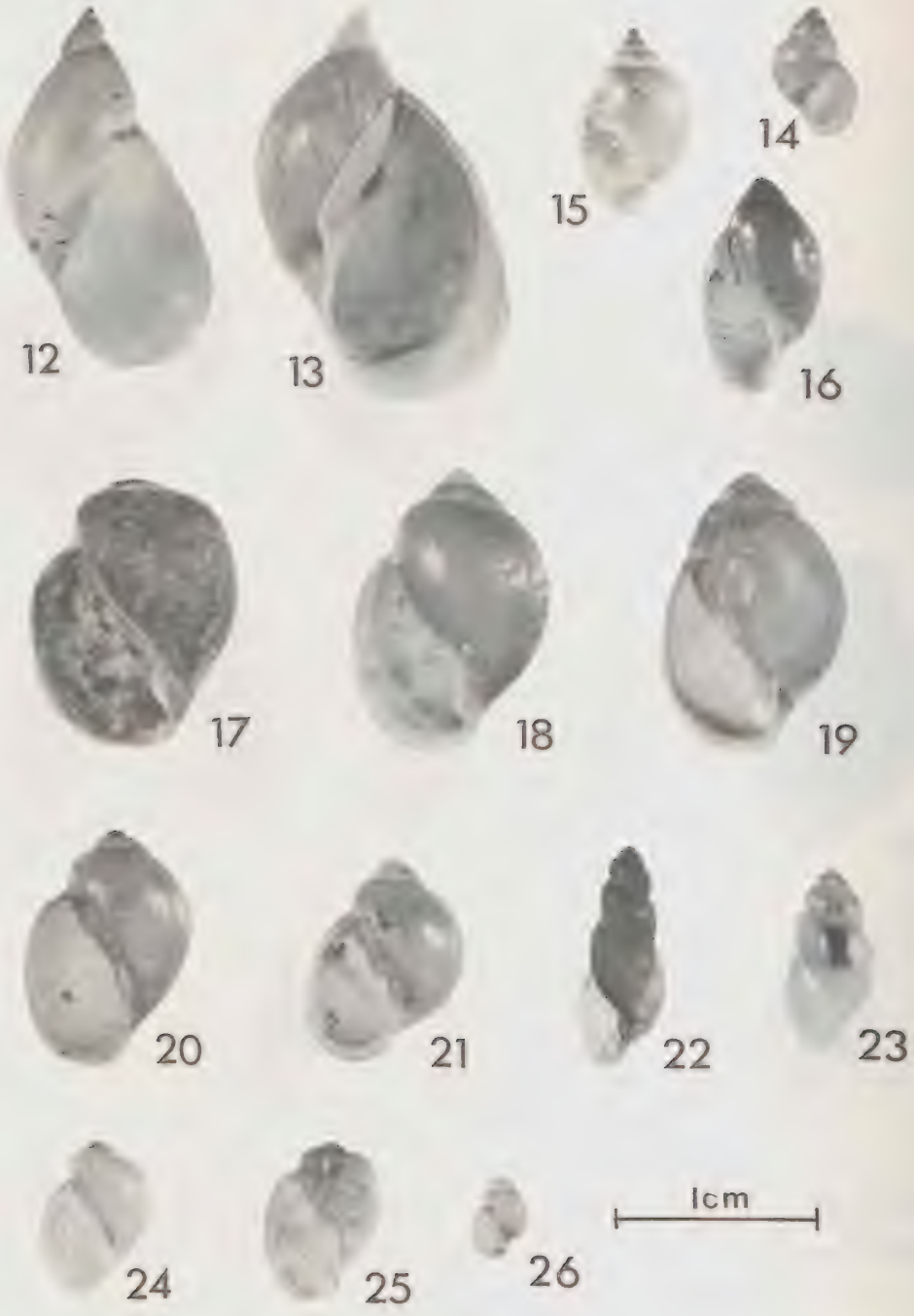
Bulinus tropicus

Bulinus truncatus

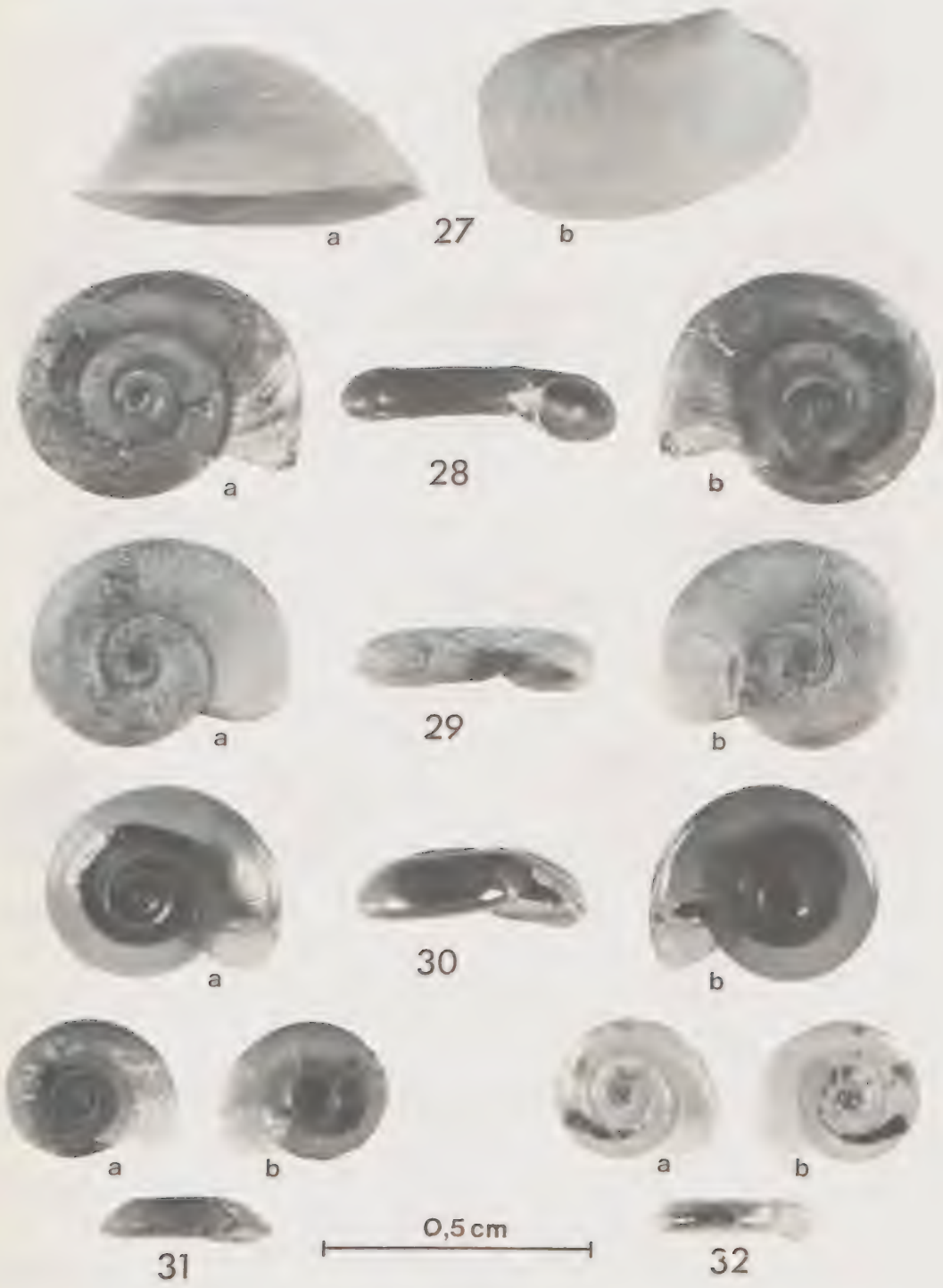
Bulinus forskalii

Distribution maps for some freshwater snails of medical or veterinary importance in Africa.

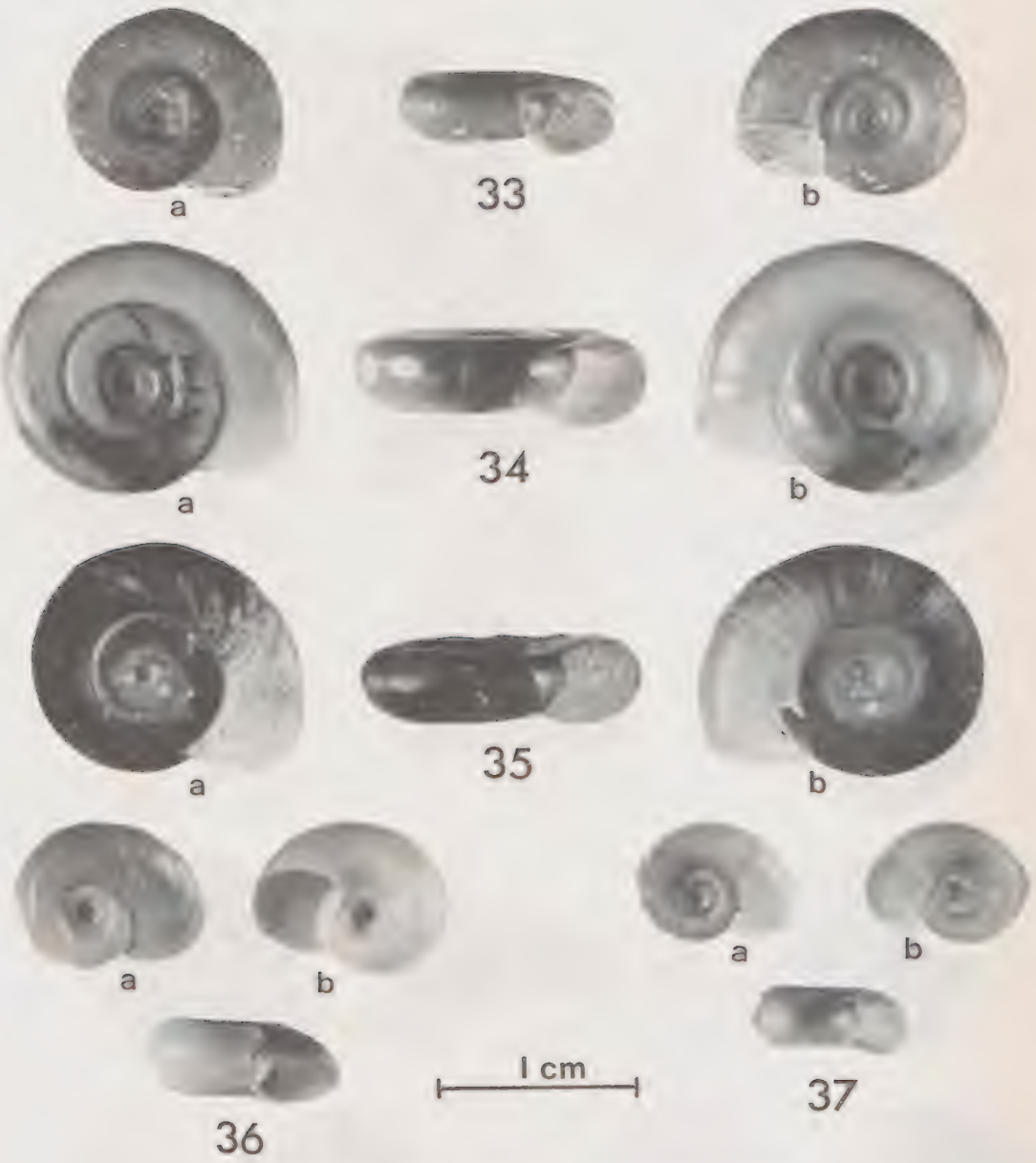
FIGS. 1-11. African freshwater shells. FIG. 1. *Lanistes ovum*. FIG. 2. *L. purpureus* (Jonas). FIG. 3. *Pila ovata*. FIG. 4a-c. *Potadoma freethi*. FIG. 5. *P. moerchi* (Reeve). FIG. 6. *Pachymelania fusca* (Gmelin). FIG. 7. *Bellamya unicolor*. FIG. 8. *Melanoides tuberculata*. FIG. 9. *Pirenella conica*. FIG. 10. *Cleopatra ferruginea*. FIG. 11. *Gabbiella humerosa* (Martens).



FIGS. 12-26. African freshwater shells. FIG. 12. *Lymnaea (Pseudosuccinea) columella*. FIG. 13. *L. (Radix) natalensis*. FIG. 14. *L. (Fossaria) truncatula*. FIG. 15. *Physella acuta*. FIG. 16. *Stenophysa marmorata* (Guilding). FIG. 17. *Bulinus africanus*. FIG. 18. *B. globosus*. FIG. 19. *B. nasutus*. FIG. 20. *B. natalensis*. FIG. 21. *B. tropicus*. FIG. 22. *B. forskalii*. FIG. 23. *B. senegalensis*. FIG. 24. *B. truncatus*. FIG. 25. *B. coulboisi*. FIG. 26. *B. reticulatus*.



FIGS. 27-32. African freshwater shells. FIG. 27. *Burnupia verreauxi* (Bourguignat). a, side view; b, spire view. FIG. 28. *Ceratophallus natalensis* (Krauss). FIG. 29. *Gyraulus costulatus* (Krauss). FIG. 30. *Segmentorbis kanisaensis* (Preston). FIG. 31. *Lentorbis junodi* (Connolly). FIG. 32. *Afrogyrus coretus* (Blainville). Figs. 28-32. a = umbilical view; b = spire view.



FIGS. 33-37. African freshwater shells. FIG. 33. *Biomphalaria pfeifferi*. FIG. 34. *B. sudanica*. FIG. 35. *B. alexandrina*. FIG. 36. *B. smithi*. FIG. 37. *B. choanomphala*. Figs. 33-37. a = umbilical view; b = spire view.

GLOSSARY

Aperture. Opening of the shell.

Bilharziasis. Also called bilharzia or schistosomiasis. Diseases in human beings and various other animals caused by flukes of the genus *Schistosoma.*

Biomphalaria. A group (genus) of pulmonate snails which are the intermediate hosts for trematode worms (*Schistosoma mansoni*) causing intestinal schistosomiasis. The most important species of *Biomphalaria* are *B. pfeifferi, B. sudanica* and *B. alexandrina.*

Blood flukes. Parasitic trematode worms, the adults of which live in the blood vessels of humans and certain other animals. Blood flukes infecting humans belong to the genus *Schistosoma.*

Bulinus. A group (genus) of pulmonate snails, some species of which are important intermediate hosts for the flukes causing urinary schistosomiasis. There are many species, the three most widespread being *Bulinus truncatus, B. globosus* and *B. forskalii.*

Classification. A method of arranging living creatures into groups. All animals and plants are arranged in certain groups, e.g., all lions belong to the same species and all leopards to another species, but these two species belong to the same genus, which is classed with other genera in a family, and so on.

Coil. Twist into circular shape.

Discoidal. Disc-shaped.

Fasciola. Liver flukes occurring in cattle and some other ruminants. Two species are found in Africa, *Fasciola hepatica* and *F. gigantica*. Their intermediate hosts are *Lymnaea (Fossaria) truncatula* and *L. (Radix) natalensis*, respectively.

Fascioliasis. A disease of cattle, sheep, etc., caused by species of *Fasciola.*

Flukes. The common name for parasitic flat worms found in the intestines, lungs, liver or blood system of mammals, birds and fishes.

Genus (plural: genera). A group of organisms consisting of a number of species closely related to one another. In the Linnaean or binomial system of nomenclature, the first name is that of the genus, the second that of the species.

Heterophyes. Flukes living in the intestine of human beings; the intermediate host is a prosobranch snail, *Pirenella conica.*

Identification key. A series of alternative choices presented as a means to identify animals or plants.

Intermediate host. An organism in which the flukes increase in number by non-sexual reproduction. Larvae of the blood flukes, for example, invade snails and thousands of new larvae are released from the snail after some time.

Intestinal schistosomiasis or bilharziasis. A disease caused by *Schistosoma mansoni* and rather rarely by *S. intercalatum*, in Africa.

Liver flukes. Flukes living in the liver, e.g., *Fasciola gigantica*, in cattle.

Lymnaea. A group (genus) of pulmonate snails which include species which are the intermediate hosts for *Fasciola* spp. The most common species of *Lymnaea* in Africa is *L. natalensis.*

Operculum. A kind of lid or cover, characteristic of prosobranch snails, which can block the aperture or opening of the shell when the body of the snail is withdrawn into the shell.

Paramphistomatidae. A family of flukes found in the stomach of cattle.

Paramphistomum. A genus of flukes belonging to the family Paramphistomatidae.

Prosobranch snails. Snails of the subclass Prosobranchia. They can be recognized by their possession of an operculum. Most prosobranch species in Africa are not of economic importance.

Pulmonate snails. Snails of the subclass Pulmonata. They lack an operculum. Many species are of great socio-economic importance. This group of snails contains the intermediate hosts of *Schistosoma* and *Fasciola.*

Schistosoma. Parasitic flukes located in the blood system of vertebrate hosts. In Africa, the following species are of medical importance: *Schistosoma mansoni, S. haematobium* and *S. intercalatum*. Two species are of veterinary importance: *S. bovis* and *S. mattheei.*

Schistosomiasis. A parasitic infection caused by members of the genus *Schistosoma.*

Species. A group of very closely related animals or plants which have a high degree of similarity and are able to breed among themselves, but not with members of another species.

Stomach flukes. Parasitic worms found in the stomach of cattle which belong to the family Paramphistomatidae.

Sutures. The line on the shell surface where two adjoining whorls meet.

Taxa. Any group in the zoological system of classification, e.g., a species, genus, family, order, subclass, etc.

Temporary pool. A waterbody which fills up with water for a few months only (in contrast to a permanent waterbody).

Tentacles. A pair of thin, elongated, sensory protrusions extending from the front of the head of the snail.

Transmitter. An infected animal which transmits a disease-producing parasite to another animal.

Urinary schistosomiasis. An infection, localized mainly in the urino-genital system, caused by *Schistosoma haematobium.*

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A GUIDE TO THE FRESHWATER SNAILS OF THE PHILIPPINES*

J.B. Burch

INTRODUCTION

Freshwater malacology is of considerable importance to the Philippines because of the human parasitic diseases transmitted by some of the country's indigenous snail species. But, in spite of this importance, there are no manuals, handbooks or guides available to help workers identify Philippine freshwater mollusks, or to place the native snail fauna into a modern frame of classification. Therefore, this guide to the identification and classification of the nation's freshwater snails is presented as a step toward strengthening malacology in the Philippines.

Appreciation is expressed to Dr. B.C. Dazo, the World Health Organization (Western Pacific Regional Office), and the Philippine Ministry of Health (Schistosomiasis Research and Control Service) for supporting these efforts.

IDENTIFICATION

Characters of the shells of freshwater gastropods are very important in species recognition and usually for generic and familial placement as well. Especially useful are the size and general form of the shell. Among the many species, the shell may take various shapes, yet, for any one species, the shell shape is usually quite constant (excepting, of course, minor clinal, populational and ecophenotypic variations exhibited by some species). The shells among the different species may vary from very elongate, to globose, depressed and discoidal. The shell may be longer than wide, or wider than long (the columella determining the antero-posterior (length/width) axis). Its coils (whorls) may turn either to the left or to the right, be round, angular, shouldered or flattened, and have shallow or impressed sutures. The shell may have few or many whorls, may lack an opening (umbilicus) at its base, or may have either a narrow or wide opening. The columella or central axial column of the shell may be either twisted or straight and may or may not end abruptly. The outer lip of the shell may be either straight or variously curved and is sometimes turned back or reflected. The surface of the shell may be marked in various ways, i.e., differentially colored or sculptured, or may be simply unicolored and smooth. The outline of the shell aperture ("mouth") may take many forms due to the shape and relation of the whorls to each other. The aperture may or may not be closed by an operculum, which itself has important recognition characters. The operculum may be round, oval or spindle-shaped, and concentric, paucispiral or multispiral, depending on the way in which it is formed.

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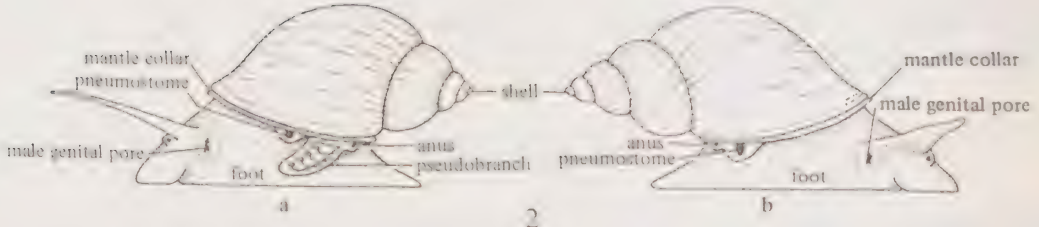

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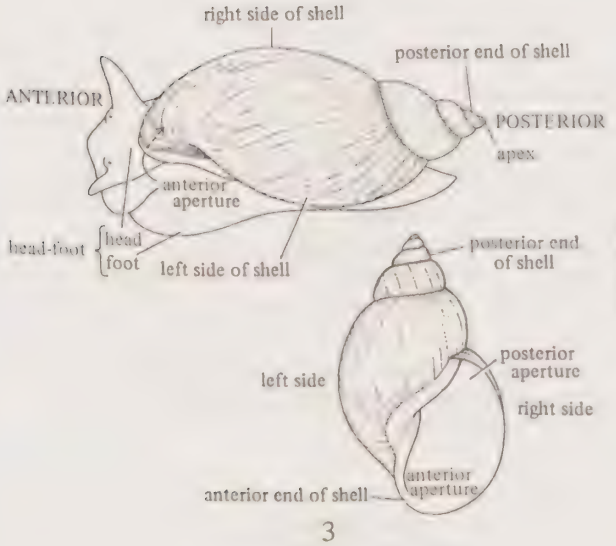

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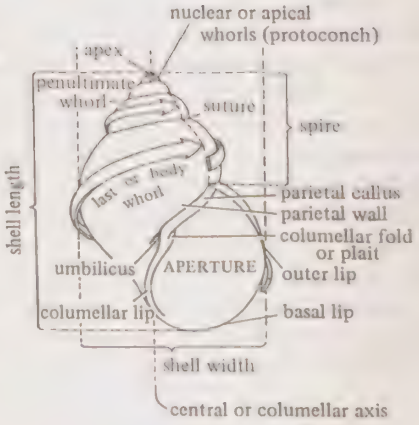

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FIG. 1. Direction of coiling of gastropod shells. **a**, Shell coiled to the left, i.e., *sinistral*; **b**, shell coiled to the right, i.e., *dextral*. FIG. 2. **a**, A snail with *sinistral* organization of its body, i.e., respiratory, excretory and reproductive openings are on the *left* side; **b**, a snail with *dextral* organization of its body, i.e., respiratory, excretory and reproductive openings are on the *right* side. FIG. 3. Orientation of the shell. FIG. 4. Shell terminology.

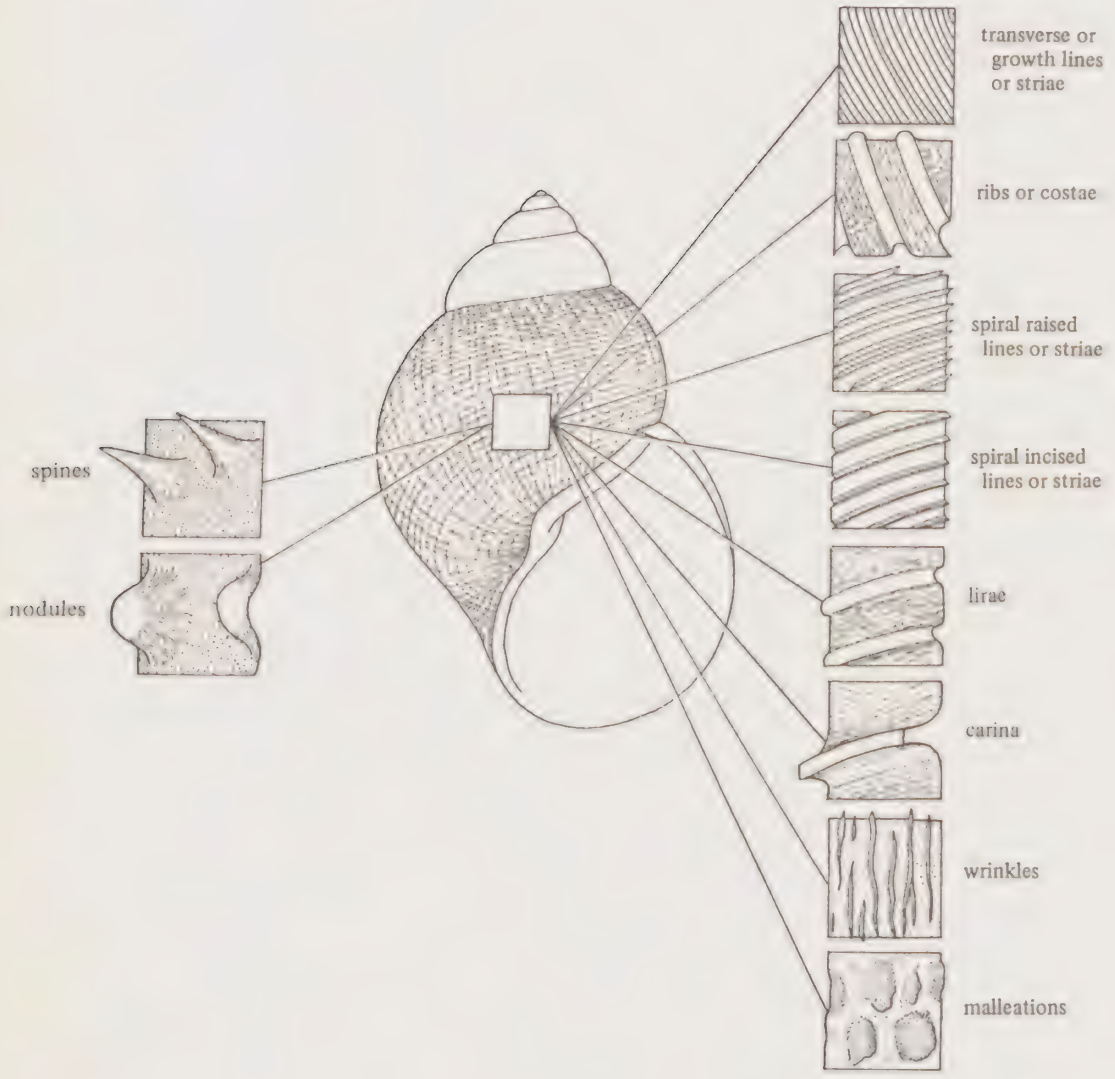


FIG. 5. Shell surface sculpture.

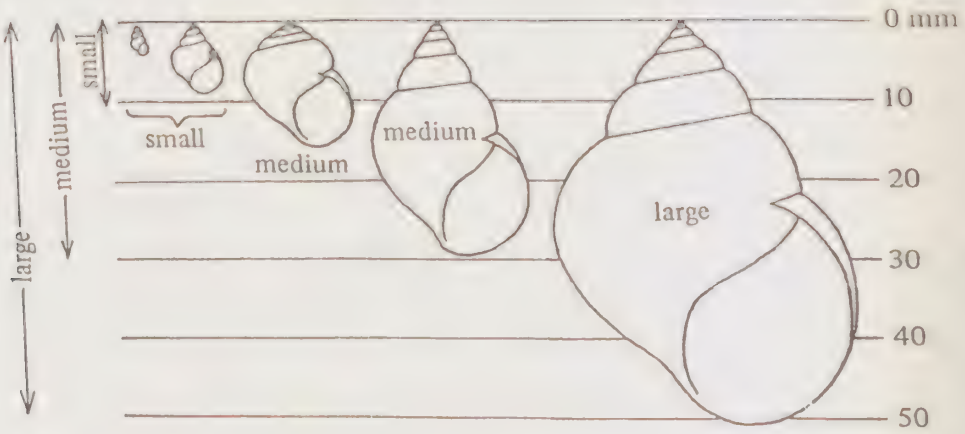
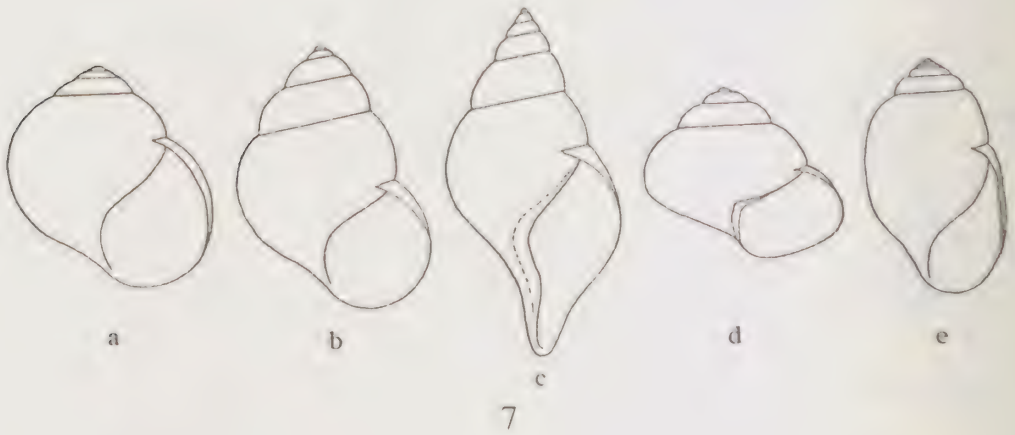


FIG. 6. Shell sizes: up to 10 mm = small; 10-30 mm = medium; over 30 mm = large.



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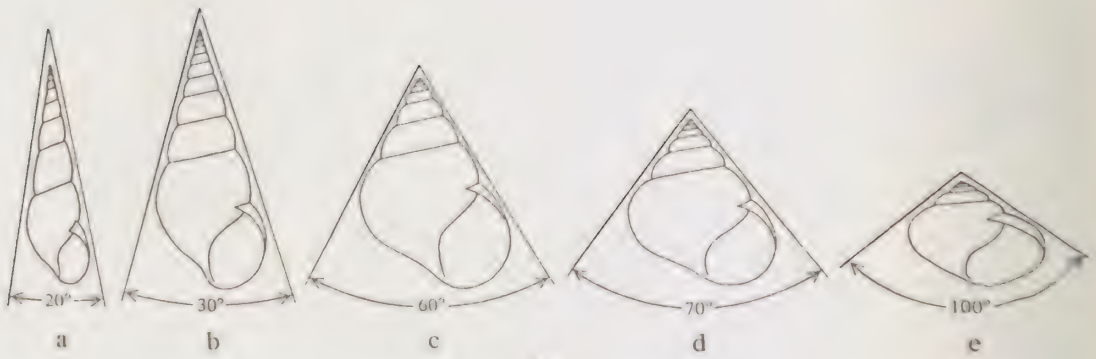

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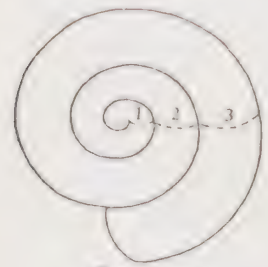
FIG. 7. Shell shapes. **a**, subglobose; **b**, oval; **c**, fusiform or spindle-shaped; **d**, turbiniform; **e**, cylindrical. FIG. 8. Shell shapes. **a**, narrowly conic; **b**, elongately conic; **c**, broadly (ovately) conic; **d**, globosely conic; **e**, depressed conic.



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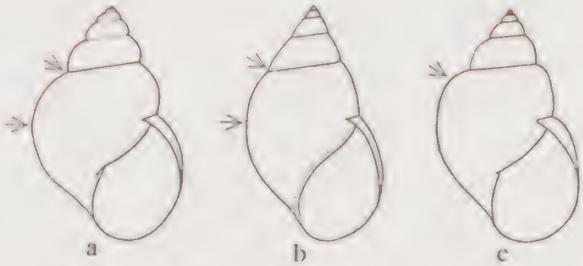

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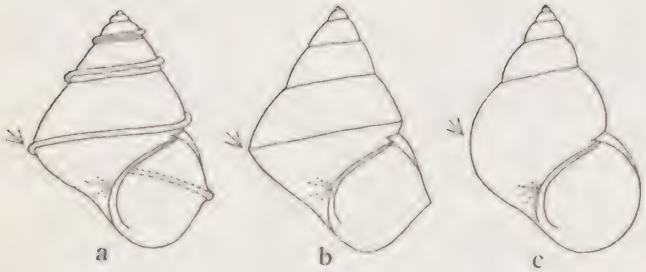

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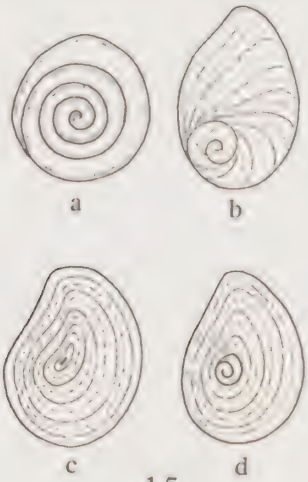

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FIG. 9. Method of counting whorls. This shell has 3¼ whorls. FIGS. 10-14. Shell terminology. FIG. 10. **a**, Shell with well-rounded whorls and indented sutures; **b**, shell with flattened whorls and shallow sutures; **c**, shell with shouldered whorls. FIG. 11. Planorbiform or discoidal shell. FIG. 12. Ancyliform or limpet-shaped shell. FIG. 13. Neritiniform shell. FIG. 14. **a**, Shell with a keel or carina; **b**, shell with angular periphery; **c**, shell with rounded periphery. FIG. 15. Types of opercula. **a**, Multispiral; **b**, paucispiral; **c**, concentric; **d**, concentric with spiral nucleus.

KEY TO THE HIGHER TAXA AND TO THE GENERA AND SUBGENERA[1]

1 Aperture of shell, in life, closed by an operculum (Fig. 16). Subclass Prosobranchia[2] 2

Aperture of shell not closed by an operculum in life. Subclass Pulmonata, Order Limnophila [= Basommatophora, in part][2] 24

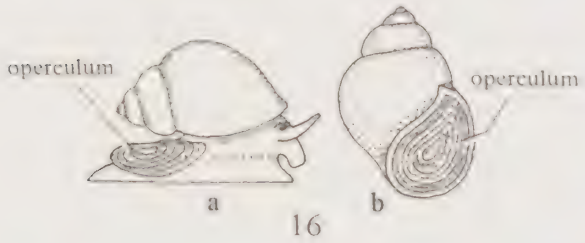

FIG. 16. An operculated snail, i.e., one which carries an operculum attached to its dorsal posterior foot. **a**, Position of the operculum when the snail is active; **b**, position of the operculum when the snail has withdrawn into its shell. (After Walter & Burch, 1957, *Mus. Zool. Univ. Mich. Circ.*, (3): 1-8.) FIG. 17. Operculum. **a**, External view; **b**, inner surface (which in life is attached to the dorsal foot).

2(1) Shell neritiniform, i.e., with relatively very large body whorl and very small coiled spire (Fig. 13); operculum with an elongate attachment process (apophysis) on its inner surface (Fig. 17). Order Neritinacea, Superfamily Neritinoidea[3], Family Neritinidae[4] 3

Shell not neritiniform, spire generally pronounced; inner surface of operculum relatively smooth, without an elongate attachment process on its inner surface. Order Mesogastropoda 9

3(2) Shell cap-shaped, nearly limpet-like, almost bilaterally symmetrical (Figs. 18-20). Genus *Septaria* 4

Shell not cap-shaped and limpet-like, but with typical gastropod spiral symmetry 6

4(3) Apical whorls extending beyond posterior apertural margin 5

Apical whorls not extending beyond posterior apertural margin (Fig. 18) . . . . . Subgenus *Navicella*

[1] Superscript numbers given in the Key (pp. 128-135) and Outline (pp. 136-137) refer to corresponding comments under Notes (p. 138).

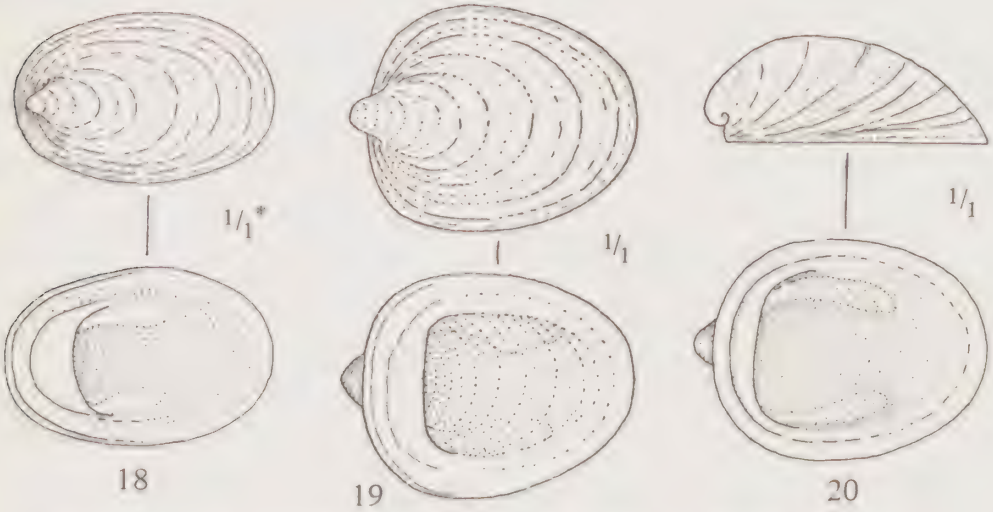

FIG. 18. *Septaria (Navicella)*. FIG. 19. *Septaria* s.s. FIG. 20. *Septaria (Sandalium)*.

5(4) Inhabitant of fast-flowing water (Fig. 19) . . . . . Subgenus *Septaria* s.s.

Inhabitant of standing water, found on plants (Fig. 20) . . . . Subgenus *Sandalium*

6(3) Shell surface with one or more spiral rows of long projecting spines (Fig. 21) . . . . . Genus *Clithon*

Shell surface without spines 7

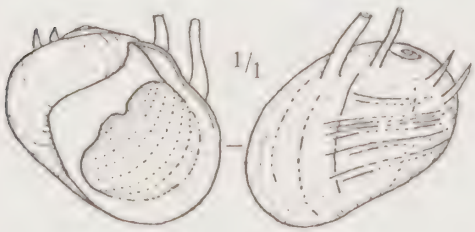

FIG. 21. *Clithon*.

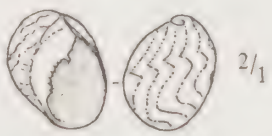

FIG. 22. *Smaragdia*.

7(6) Adult shell large, more than 1 cm and up to 3 cm or more in length. Genus *Neritina* 8

Adult shell small, less than 1 cm in length (Fig. 22) . . . . . Genus *Smaragdia*, Subgenus *Smaragdella*

*Size of figure to actual size of specimen is given throughout the key by a ratio: 1/1 = natural size; 2/1 = twice natural size; 3/1 = enlarged three times; etc.

8(7) Groove present where the right apertural lip meets the parietal shell wall; apophysis on operculum well developed (Fig. 23) . . . . . Subgenus *Neritina* s.s.

Right apertural lip meets the parietal shell wall without producing a groove; apophysis on operculum reduced to a plate (Fig. 24) . . . . . Subgenus *Neritona*

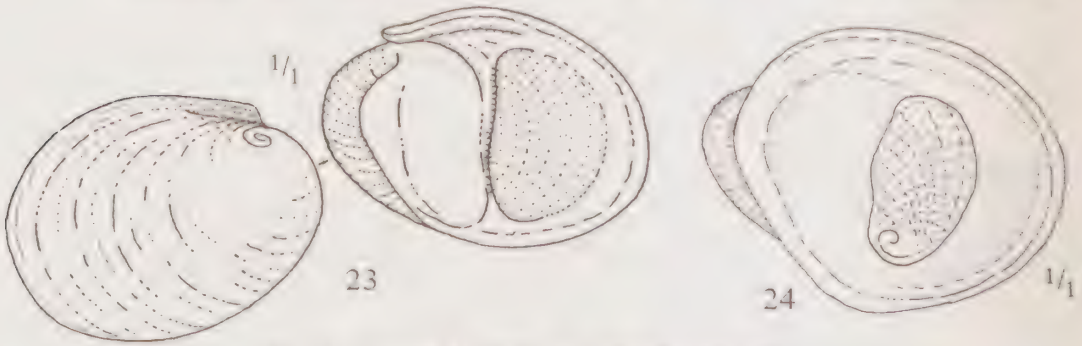

FIG. 23. *Neritina* s.s. FIG. 24. *Neritina (Neritona).*

9(2) Adult shell large, more than 1 cm and up to 7 cm or more in length 10

Adult shell small, less than 1 cm in length 22

10(9) Shell spire elongate, more than 1/2 the total shell length 11

Shell spire depressed, less than 1/2 the total shell length. Superfamily Ampullarioidea (in part) (Fig. 25), Family Ampullariidae . . . . . Genus *Pila*

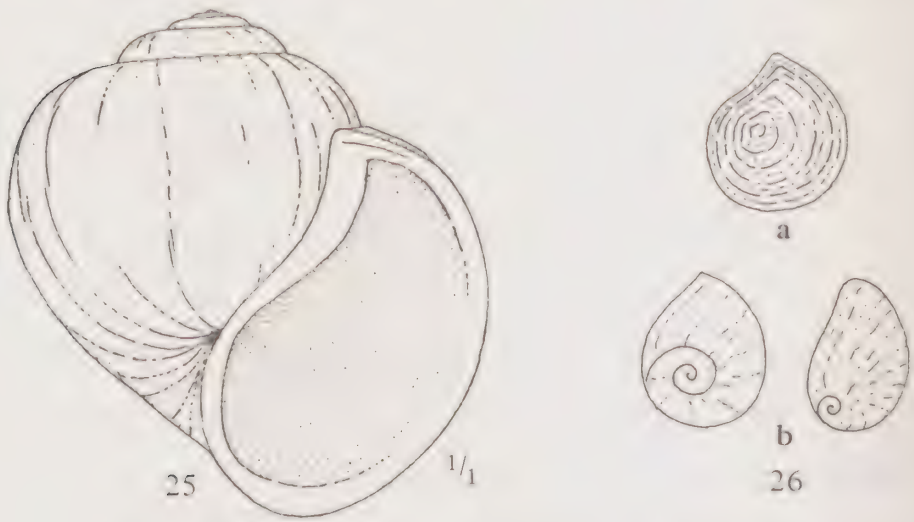

FIG. 25. *Pila*. FIG. 26. Opercula. a, Concentric; b, paucispiral.

11(10) Operculum concentric (Fig. 26a). Superfamily Ampullarioidea (in part). Family Viviparidae[5] 12

Operculum paucispiral (Fig. 26b). Superfamily Vermetoidea 16

12(11) Shell carinate, with only one carina, which is at the circumferal periphery of the whorls (Figs. 27, 28). Genus *Angulyagra* 13

Shell with or without carinae, but if present the carinae are usually subobsolete and more than just one, but if with only one carina it is not usually at the circumferal periphery of the whorls 14

13(12) Carina continuous, with spines (Fig. 27) . . . . . Subgenus *Angulyagra* s.s.

Carina with periodic hollow outwardly-turned spines (Fig. 28) . . . . . Subgenus *Acanthotropis*

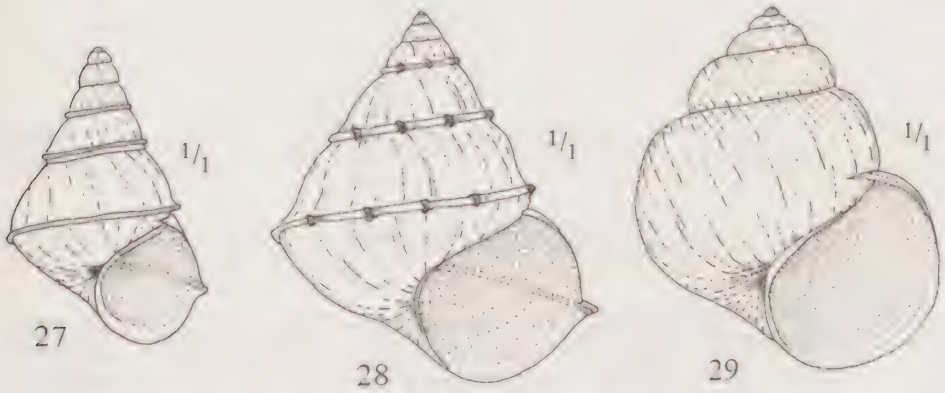

FIG. 27. *Angulyagra* s.s. FIG. 28. *Angulyagra (Acanthotropis)*. FIG. 29. *Cipangopaludina*.

14(12) Adult shells large, globose, 4 cm or longer in length (Fig. 29) . . . . . Genus *Cipangopaludina*[6]

Adult shells medium to large, but if large (4 cm or more in length) the shells are elongate, conical, turreted and with carinae 15

15(14) Shell globose, generally with numerous close-set keels, imperforate (Fig. 30) . . . . . Genus *Taia*, Subgenus *Torotaia*

Shell globose or turbinate to broadly conical or turreted; if the shell is globose or turbinate it is generally smooth, but if carinae are present they are usually obsolete or subobsolete; shell narrowly umbilicate, perforate or imperforate (Fig. 31) . . . . . Genus *Bellamya*

FIG. 30. *Taia*.

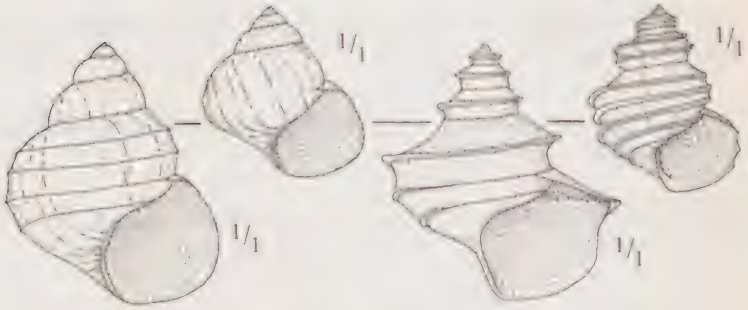

FIG. 31. *Bellamya*.

16(11) Shell ovate or broadly conical, aperture ovate, rather large, nearly 1/2 the total shell length. Family Paludomidae (Fig. 32) . . . . . Genus *Paludomus*

Shell elongate, narrowly conical. Family Thiaridae 17

FIG. 32. *Paludomus*.

17(16) Adult shell large, more than 4 cm and up to 7 cm or more in length, elongately conic; surface sculptured with ribs, spiral cords or carinae, or low spines, or with two or more of these features in combination (Fig. 33) . . . . . Genus *Brotia*

Shell medium (1.5-3 cm in length) to large (3.5-7+ cm in length), but if large the shell is without spines, very narrowly conic and with the first part of the spire almost needle-like (if not eroded); shells smooth or variously sculptured 18

18(17) Shell surfaces variously sculptured, but without spines 20

Shell surface sculpture includes spines (Figs. 34, 35). Genus *Thiara* 19

19(18) Spines prominent, projecting outward; periostracum dark green (Fig. 34) . . . . . Subgenus *Tiaropsis*

Spines not prominent generally, situated as posterior projections of the surface ribs; periostracum dark brown or black (Fig. 35) . . . Subgenus *Plotiopsis*

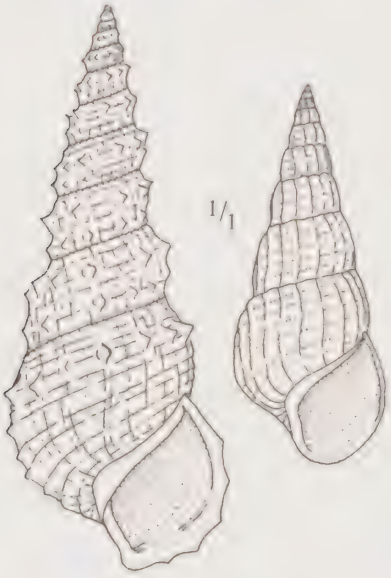

FIG. 33. *Brotia*.

FIG. 34. *Thiara (Tiaropsis)*.

FIG. 35. *Thiara (Plotiopsis)*.

20(18) Shell surface with ribs, lirae, or spiral striae and cords, but without tubercles (Fig. 36) . . . . . Genus *Melanoides*

Shell surface with tubercles, which may or may not be located on ribs 21

21(20) Shell elongately conic (Fig. 37) . . . . . Genus *Tarebia*

Shell narrowly conic (Fig. 38) . . . . . Genus *Sermyla*

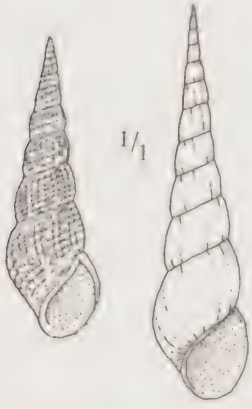

FIG. 36. *Melanoides* s.s.

FIG. 37. *Tarebia*.

FIG. 38. *Sermyla*.

22(9) Shell globose, aperture and spire nearly equal in length (Fig. 39); operculum concentric (Fig. 15c), calcareous. Superfamily Ampullarioidea (in part). Family Bithyniidae . . . . . Genus *Petroglyphus*

Shell elongate, spire length noticeably greater than aperture length (Figs. 40, 41); operculum paucispiral (Fig. 15b), corneous. Superfamily Truncatelloidea 23

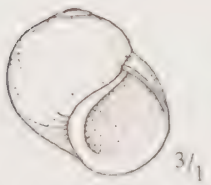

FIG. 39. *Petroglyphus*.

FIG. 40. *Oncomelania*.

FIG. 41. *Stenothyra*.

23(22) Entire body whorl and aperture follow the shell's initial spiral symmetry and gradual increase in size (Fig. 40). Family Pomatiopsidae . . . Genus *Oncomelania*

Last part of body whorl and aperture deflected and reduced in size (Fig. 41). Family Stenothyridae . . . . . Genus *Stenothyra*

24(1) Shell cap-like (limpet-shaped; ancyliform), not coiled (Fig. 42). Superfamily Ancyloidea (in part). Family Ancylidae . . . . . Genus *Pettancylus*[7]

Shell coiled, not cap-like 25

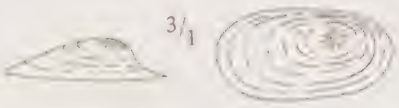

FIG. 42. *Pettancylus*.

25(24) Shell planorboid (planispiral; discoidal), coiled in one plane (Figs. 43-45). Superfamily Ancyloidea (in part). Family Planorbidae (in part) 26

Shell elongate, coils not restricted to one plane (Figs. 46-49) 28

26(25) Adult shell small, less than 1 cm in diameter 27

Adult shell large, more than 1 cm in diameter (Fig. 43) . . . . Genus *Indoplanorbis*

FIG. 43. *Indoplanorbis.*

FIG. 44. *Helicorbis.*

FIG. 45. *Gyraulus.*

27(26) Shell glossy, periphery angular (Fig. 44) . . . . . Genus *Helicorbis*

Shell dull, periphery rounded (Fig. 45) . . . . . Genus *Gyraulus*

28(25) Shell coiled to the left (sinistral) (Fig. 46). Superfamily Ancyloidea (in part). Family Planorbidae (in part) . . . . . Genus *Physastra*

Shell coiled to the right (dextral) (Figs. 47-49). Superfamily Lymnaeoidea. Family Lymnaeidae[8] 29

FIG. 46. *Physastra.*

FIG. 47. *Bullastra.*

FIG. 48. *Austropeplea.*

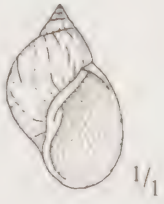

FIG. 49. *Radix.*

29(28) Spire depressed, very short, flush with or hardly raised above the body whorl (Fig. 47) . . . . . Genus *Bullastra*

Spire elongate, pointed 30

30(29) Columella generally straight, without a fold or plait at the apertural margin (Fig. 48) . . . . . Genus *Austropeplea*

Columella generally twisted, making a fold or plait at the apertural margin (Fig. 49) . . . . . Genus *Radix*

OUTLINE OF CLASSIFICATION[1]

Class GASTROPODA Cuvier 1797 (Duméril 1806)

Subclass PROSOBRANCHIA Milne Edwards 1848 [Streptoneura Spengel 1881]

Order NERITINACEA Rafinesque 1815

Superfamily Neritinoidea[3] Rafinesque 1815

Family **NERITINIDAE**[4] Rafinesque 1815
- Genus *Clithon* Montfort 1810 (*Nerita corona* Linnaeus)*
- Genus *Neritina* Lamarck 1816 (*Nerita pulligera* Linnaeus)
  - Subgenus *Neritina* s.s.
  - Subgenus *Neritona* Martens 1869 (*Neritina labiosa* Sowerby)
- Genus *Septaria* Férussac 1807 (*Patella borbonica* Bory Saint Vincent)
  - Subgenus *Septaria* s.s.
  - Subgenus *Navicella* Lamarck (in Bruguière, etc.) 1816 (*Navicella tesselata* Lamarck)
  - Subgenus *Sandalium* Schumacher 1817 (*Sandalium picta* Schumacher)
- Genus *Smaragdia* Issel 1869 (*Neritina feulleti* Audouin)
  - Subgenus *Smaragdella* H.B. Baker 1923 (*Neritina souverbiana hellvillensis* Crosse)

Order MESOGASTROPODA Thiele 1927 [Taenioglossa Troschel 1848; Monotocardia Mörch 1865]

Superfamily Ampullarioidea Guilding 1828 [Ampullariacea; Cyclophoroidea or Cyclophoracea]

Family **VIVIPARIDAE** Gray 1847[5]
- Subfamily Bellamyinae Rohrback 1937
  - Genus *Angulyagra* Rao 1931 (*Paludina oxytropis* Benson)
    - Subgenus *Angulyagra* s.s.
    - Subgenus *Acanthotropis* Haas 1939 (*Vivipara partelloi* Bartsch)
  - Genus *Bellamya* Jousseaume 1886 (*Paludina bellamya* Jousseaume)
  - Genus *Cipangopaludina* Hannibal 1912[6] (*Paludina malleata* Reeve)
  - Genus *Taia* Annandale 1818 (*Vivipara naticoides* Theobald)
    - Subgenus *Torotaia* Haas 1939 (*Vivipara clemensi* Bartsch)

Family **AMPULLARIIDAE** Guilding 1828
- Genus *Pila* Bolten (in Röding) 1798 (*Helix ampullacea* Linnaeus)

Family **BITHYNIIDAE** Gray 1857
- Genus *Petroglyphus* Moellendorff (in Quadras & Moellendorff) 1894 (*Petroglyphus mindanavicus* Moellendorff)

Superfamily Truncatelloidea Gray 1840 (Rissooidea H. & A. Adams 1954)

Family **POMATIOPSIDAE** Stimpson 1865
- Genus *Oncomelania* Gredler 1881 (*Oncomelania hupensis* Gredler)

*Type species are placed in parentheses after each generic-group name.

Family **STENOTHYRIDAE** Fischer 1887
Genus *Stenothyra* Benson 1856 (*Nematura deltae* Benson)

Superfamily Vermetoidea Rafinesque 1815 [Cerithioidea Flemming 1822]

Family **PALUDOMIDAE** Gill 1871
Genus *Paludomus* Swainson 1840 (*Melania conica* Gray)

Family **THIARIDAE** Troschel 1857
Genus *Brotia* H. Adams 1866 (*Melania pagodula* Gould)
Genus *Melanoides* Olivier 1804 (*Melanoides fasciolata* Olivier = *Nerita tuberculata* Müller)
Genus *Sermyla* H. & A. Adams 1854 (*Melania granifera* Lamarck)
Genus *Tarebia* H. & A. Adams 1854 (*Melania tornatella* Lea)
Genus *Thiara* Röding 1798 (*Helix amarula* Linnaeus)
Subgenus *Plotiopsis* Röding 1798 (*Buccinum scabra* Müller)
Subgenus *Tiaropsis* Brot 1870 (*Melania winteri* Busch)

Subclass PULMONATA Cuvier 1817

Order LIMNOPHILA [Basommatophora, in part]

Superfamily Lymnaeoidea Rafinesque 1815

Family **LYMNAEIDAE** Rafinesque 1815[8]
Genus *Austropeplea* Cotton 1942 (*Limnea papyracea* Tate)
Genus *Bullastra* Bergh 1901 (*Bullastra velutinoides* Bergh = *Lymnaea cumingiana* Pfeiffer)
Genus *Radix* Montfort 1810 (*Radix auriculatus* Montfort = *Helix auricularia* Linnaeus)

Superfamily Ancyloidea Rafinesque 1815

Family **PLANORBIDAE** Rafinesque 1815
Subfamily Planorbinae Rafinesque 1815
Tribe Planorbini Rafinesque 1815
Genus *Gyraulus* Charpentier 1837 (*Planorbis hispidus* Draparnaud = *Planorbis albus* Müller)
Tribe Miratestini Sarasin 1897
Genus *Physastra* Tapparone-Canefri 1883 (*Physa (Physastra) vestita* Tapparone-Canefri)
Tribe Segmentini F.C. Baker 1945
Genus *Helicorbis* Benson 1855 (*Planorbis (Helicorbis) umbilicalis* Benson)
Subfamily Bulininae Herrmannsen 1847 [emend.]
Genus *Indoplanorbis*[6] Annandale & Prashad 1920 (*Planorbis exustus* Deshayes)

Family **ANCYLIDAE** Rafinesque 1815
Subfamily Ferrissinae Walker 1917
Genus *Pettancylus* Iredale 1943[7] (*Ancylus tasmanicus* Tenison-Woods)

NOTES

[1] In a dichotomous "key" such as the one presented here, the reader with a snail to identify is presented with a successive series of two opposing choices ("couplets") about one or more characters (usually morphological) possessed by the animals whose identity is to be determined. In each successive couplet of the key, only one of the opposing sets of characters should fit the specimen in question, the choice of which leads the reader to the next couplet of opposing choices. This procedure is followed until a couplet leads the reader to a taxon name (in this key, to a genus or subgenus) rather than the number of another couplet. This taxon name identifies the animal in question.

[2] Higher taxonomic categories (subclass, order, superfamily, family, subfamily, tribe) are given at the appropriate places in the key. However, the couplet characters are for the purpose of identifying only the Philippine freshwater snails, and therefore the characters used in the couplets are not necessarily diagnostic for the higher taxonomic categories on a worldwide basis.

[3] The ending *-oidea* for superfamilies is recommended by the International Commission on Zoological Nomenclature instead of *-acea*, which is commonly used in malacological literature.

[4] Neritidae auct., *non* Rafinesque, is a junior synonym of Neritinidae Rafinesque 1815.

[5] In older literature, all Philippine Viviparidae were placed in the Holarctic genus *Viviparus*. However, members of the subfamily Viviparinae to which that genus belongs do not occur in southern and southeastern Asia or Australasia. The classification used here follows Haas (1939, *Zool. Ser. Field Mus. nat. Hist.*, 24(8): 93-103), although it is realized that future research on Philippine Viviparidae undoubtedly will modify Haas' classification and nomenclature.

[6] Artificially introduced by man in recent times.

[7] Freshwater limpets, undoubtedly *Pettancylus*, have been found by Dr. B.C. Dazo in Leyte (Dazo, personal communication).

[8] In many reports, all lymnaeids in the Western Pacific are included in the Holarctic genus *Lymnaea*. However, the southern and southeastern Asian and Australasian lymnaeids belong to a different stock from the Holarctic *Lymnaea stagnalis*, the type species of the genus *Lymnaea*. Two species groups (genera or subgenera) of Lymnaeidae occur in the Western Pacific region, *Radix* and *Austropeplea*. Additionally, *Bullastra*, which was named for the Philippine species *cumingiana*, may prove to belong to a third group generically distinct from *Radix* and *Austropeplea*; or it may be congeneric with one of the latter two. If *Bullastra* is shown to be congeneric with *Austropeplea*, then *Bullastra* will replace that name.

GLOSSARY

Ancyliform. Having a shell shape like the gastropod genus *Ancylus* or any of the Ancylidae, i.e., a low, uncoiled cone.

Angular, angulate. Having an angle (or having the tendency to form an angle), rather than a round contour.

Angulation. A low ridge; edge along which two surfaces in different planes meet at an angle.

Aperture. The opening or "mouth" of a snail shell through which the head-foot protrudes when the snail is active.

Apex. The tip of a gastropod shell farthest from the aperture.

Apophysis. A calcareous protuberance or elongate structure, such as that on the inner side of a neritinid operculum.

Axial. Parallel to the axis or columella of a shell, i.e., transverse to the direction of the shell's spiral coil.

Bilaterally symmetrical. Having a symmetry in which the body is divided along a longitudinal axis into two equal sides which are mirror images of each other.

Body whorl. The last complete whorl or volution of a spiral snail shell, measured from the outer lip back to a point immediately above the outer lip. It is normally the largest whorl of the shell and is called the body whorl because it encloses the greatest part of the snail's body.

Calcareous. Composed of carbonate of lime (calcium carbonate).

Carina (pl. carinae). A sharp spiral edge, ridge or "keel" on the outer shell surface.

Carinate. Having one or more sharp spiral edges, ridges or keels on the outer shell surface.

Class. A higher taxonomic category or group between the order and phylum in the hierarchy of animal classification. Each class contains one or more orders. The living mollusks are divided into seven classes, the Gastropoda (snails, slugs, limpets, etc.), Bivalvia or Pelecypoda (clams, mussels, oysters, etc.), Scaphopoda (tusk and tooth shells), Aplacophora (includes solenogasters), Monoplacophora, Polyplacophora (chitons) and Cephalopoda (squid, cuttlefish, octopuses).

Classification. The arrangement of different kinds of organisms into groups, reflecting relationships, and the groups into a scheme or system, usually hierarchial in nature.

Columella. The internal column around which the whorls revolve; the axis of a spiral shell.

Concentric. Having the same center, e.g., the nucleus, and expanding outward in parallel (i.e., equidistant) lines, as in the lines of growth of an operculum.

Conical. Shaped like a cone, i.e., tapering evenly from a wide, circular base to a point.

Cord. A raised, coarse, rounded spiral ridge on a gastropod shell; larger than striae, but smaller than lirae.

Corneous. Resembling horn or consisting of a horn-like material.

Costa (pl. costae). A transverse rib or rounded ridge of considerable size on the surface of a shell.

Costate. Refers to a shell in which the surface is sculptured with heavy, regular transverse ridges or ribs.

Depressed. Flattened dorso-ventrally or postero-anteriorally, as the spire of a shell.

Dextral. Wound or spiraled to the right; with a clockwise spiral. When the shell aperture faces the observer and the shell apex is directed upward, the aperture is on the right.

Discoidal. Round and flat like a disc.

Elongate. Lengthened; extending length-wise; especially higher than wide.

Elongately conic. Designation for a gastropod shell with a spire angle of about 30° (± 5°).

Family (adj., familial). A taxonomic group of genera sharing certain basic features that set them off from other such groups of genera. The family is a level of classification between the genus and the order. Names of families end in *-idae.*

Gastropod. A member of the molluscan class Gastropoda; a snail, slug, limpet, etc.

Genus (pl. genera; adj., generic). A basic category of biological classification above the species level which contains (usually) two or more related species which share certain features. A few genera are monotypic, i.e., contain only one species.

Globose. Globular or spherical; approaching a globe or sphere in shape.

Glossy. Smooth and shining; highly polished.

Growth lines. Minute lines on the outer shell surface indicating minor rest periods during growth. Not to be confused with the major "rest marks" or varices, caused by prolonged growth arrest (as during winter).

Imperforate. Refers to a spiral gastropod shell which has no opening or external cavity at its base. In such a case, the inner sides of the coiled whorls are appressed, leaving no cavity, or, if they are not appressed and a cavity is formed, then its opening is completely covered by a callus or the reflected columellar apertural lip.

Keel. A sharp edge; carina.

Limpet. A gastropod with a low, conical, unspiraled (or nearly so) shell.

Lip. Edge of the aperture of a shell; peristome; peritreme.

Lira (pl. lirae). A large ridge, specifically a spiral ridge, on the outer surface of a snail shell.

Lirate. Refers to a shell with spiral ridges on its external surface.

Multispiral. Refers to an operculum in which there are numerous, very slowly enlarging spirals, coils or whorls.

Narrowly conic. Designation for a gastropod shell with a spire angle of about 20° (± 5°).

Neritiniform. Shaped like *Neritina*, i.e., subglobose or hemispherical, with few rapidly enlarging whorls, very reduced spire, and a heavily calloused and expanded parietal apertural margin.

Obsolete. Rudimental; poorly developed; obscure; indistinct; atrophied.

Operculum (pl. opercula). A corneous or calcareous plate borne on the dorsal posterior foot of prosobranch snails which closes the aperture when the snail withdraws into its shell.

Order (adj., ordinal). A higher taxonomic category or group between the family and class in the hierarchy of animal classification. Each order contains a group of families related to one another by common morphological characteristics.

Oval, ovate. In the shape of the longitudinal section of a hen's egg, i.e., oblong and curvilinear, with one end narrower than the other.

Paucispiral. Refers to an operculum in which there are few rapidly enlarging spirals, coils or whorls.

Perforate. Refers to a spiral gastropod shell which has a very narrow perforation at its base, formed where the inner sides of the coiled whorls do not join.

Periostracum. The thin proteinaceous external layer covering most mollusk shells.

Periphery. The edges of a shell as seen in outline.

Plait. A fold on the columella.

Planispiral. Coiled in one plane.

Planorboid. Having a shell shape like the gastropod genus *Planorbis*, i.e., coiled in one plane.

Rib. A transverse elevation or ridge of considerable size on the surface of a shell; costa.

Rounded. Having a more or less evenly curved contour, in contrast to being angular.

Sculpture. The natural surface markings, other than those of color, usually found on snail shells, and often furnishing identifying marks for species recognition.

Sinistral. Wound or spiraled to the left; with a counter-clockwise spiral. When the shell aperture faces the observer and the shell apex is directed upward, the aperture is on the left.

Species (pl. species; adj., specific). A taxonomic group comprising the same 'kinds' of closely related individuals potentially able to breed with one another, and unable to breed with other 'kinds'.

Spiral. Winding, coiling or circling around a central axis; winding around a fixed point and continually receding from it; the form of the shell of most snails.

Spiral sculpture. Surface markings of a snail shell which pass continuously around the whorls more or less parallel to the suture.

Spire. The whorls of a snail shell, excepting the last or body whorl. The spire is measured as the distance (parallel to the columella) from the suture where the apertural lip meets the body whorl to the shell apex.

Stria (pl. striae). A slight superficial spiral groove or furrow on the outer shell surface, or a fine spiral threadlike line or streak. Commonly used also, in a less precise sense, for raised spiral ridges on the shell surface.

Striate. Refers to a shell having spiral incised lines on its surface. Also used, less precisely, for shells with spiral raised lines, or for shells covered with fine transverse lines.

Subclass. A higher taxonomic category or group between the order and class in the hierarchy of animal classification. Subclasses are used when it is necessary to divide a class into more than one group of orders. The subclasses of the Class Gastropoda (snails, slugs, limpets) are the Prosobranchia (gill breathers; gills anterior to the heart), Opisthobranchia (generally gill breathers; gills, when present, posterior to the heart) and Pulmonata (lung breathers).

Subfamily (adj., subfamilial). A taxonomic category or group between the genus and family in the hierarchy of animal classification. Subfamilies are used when it is necessary to divide a family into more than one group of closely related genera. The subfamily is therefore a subordinate category to the family. Each subfamily contains one or more genera. Names of subfamilies end in *-inae*.

Subgenus (pl. subgenera; adj., subgeneric). A taxonomic category or group between the species and genus in the hierarchy of animal classification. Subgenera are used when it is necessary to divide a genus into more than one group of closely related species. The subgenus is therefore a subordinate category to the genus. Each subgenus contains one or more species.

Subspecies (pl. subspecies; adj., subspecific; syn., race). One or more populations of a species which inhabit a distinct geographic area and which share morphological features setting them off from other populations of the species.

Superfamily. A taxonomic category or group between the family and order in the hierarchy of animal classification. Superfamilies are used when it is necessary to divide an order into more than one group of closely related families. Names of superfamilies end in *-oidea* (although it also has been common practice in malacology to use *-acea*).

Taxon (pl. taxa). Any taxonomic group, e.g., a race, subspecies, species, genus, family, order, etc.

Taxonomy (adj., taxonomic). The practice, study, methodology, science, etc., of dealing with kinds of organisms.

Tribe. A taxonomic category or group between the genus and subfamily in the hierarchy of animal classification. Tribes are used when it is necessary to divide a subfamily into more than one group of closely related genera. The tribe is therefore a subordinate category to the subfamily. Each tribe contains one or more genera. Names of tribes end in *-ini.*

Tubercle. A nodule or small eminence, such as a solid elevation occurring on the shell surface of some gastropods.

Tuberculate. Covered with tubercles or rounded knobs.

Turbinate, turbiniform. Shaped like a turban; refers to a shell in which the whorls decrease rapidly in diameter and taper broadly from a circular base to the apex.

Turreted; turriform. Tower-shaped; spire whorls shouldered, forming a regularly stepped outline.

Umbilicate. Refers to a spiral gastropod shell which has an opening or cavity at its base, and more specifically to one in which the opening is more than a very narrow perforation. This cavity is formed in those shells in which the inner sides of the coiled whorls do not join.

Whorl (spelled 'whirl' in early literature). One complete turn or coil of a spiral gastropod shell.

J.B. BURCH

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NEWS AND ANNOUNCEMENTS

* * * * *

MALACOLOGICAL SOCIETY OF THE PHILIPPINES. – On May 30, 1980, an organizational meeting of the Malacological Society of the Philippines was held at the Department of Zoology of the University of the Philippines. Founding members were malacologists, zoologists and parasitologists of the Schistosomiasis Control and Research Services, Ministry of Health; Department of Zoology and Institute of Public Health, University of the Philippines, respectively. Advisers of the Society are Bonifacio C. Dazo of the World Health Organization, Manila, and J.B. Burch of The University of Michigan, Ann Arbor.

The officers and members of the Malacological Society of the Philippines are as follows. President, Ruben Umaly, Department of Zoology, University of the Philippines; Secretary, Edith Alikpala, Department of Zoology, University of the Philippines; Treasurer, Mary Anne Batalla, Natural Science Research Center. Regional Officers: Edgardo Erce, Jose Espejo, Jr., Obdulla Morallos, Albert Oyco, Mercedes Palpallatoc. Members: Purita P. Aganon, Schistosomiasis Control Team (SCT), Trinidad, Bohol; Edith P. Alikpala; Lily M. Alquiza, Institute of Public Health, University of the Philippines; Arlita Z. Aquitania, Schistosomiasis Control and Research Services (SCRS), Manila; Eva S. Asistores, SCT, Malaybalay, Bukidnon; Celia M. Austria, University of the Philippines College at Baguio; Mary Anne S. Batalla; Nestor M. Beltran, SCT, Marbel, South Cotabato; J.B. Burch; Jaime J. Cabrera, National Museum, Manila; Elvira M. Cala, SCT, Malaybalay, Bukidnon; Bonifacio C. Dazo; Edgardo S. Erce, SCT, Tagum, Davao; Jose Espejo, Jr., SCT, North Cotabato; Consuelo D. Guingab, SCRS, Palo, Leyte; Nonette L. Jueco, Institute of Public Health, University of the Philippines; Ayolani V. de Lara, Natural Science Research Center, University of the Philippines; Ramon P. Luber, Natural Science Research Center, University of the Philippines; Ronald R. Matias, Department of Zoology, University of the Philippines; Avelina R. Mojica, SCT, Tandag, Surigao del Sur; Obdulia G. Morallos, SCT, Catarman, Northern Samar; Mario C. Nadal, SCT, San Francisco, Agusan del Sur; Alberto P. Oyco, SCT, Victoria, Oriental Mindoro; Mercedes H. Palpallatoc, SCT, Bonifacio, Misamis Occidental; Lilia B. Querubin, Natural Science Research Center, University of the Philippines; Blessy Racimo, SCRS, Manila; Ma. Isabel Ramos, Natural Science Research Center, University of the Philippines; Evangeline Suelo, SCRS, Palo, Leyte; Wilfred U. Tiu, Institute of Public Health, University of the Philippines; Ruben C. Umaly; Ferdinand Vergard, SCT, Irosin, Sorsogon. – RUBEN C. UMALY

SOUTHEAST ASIAN CENTER FOR APPLIED MALACOLOGY ESTABLISHED AT MAHIDOL UNIVERSITY, BANGKOK, THAILAND. – The Center for Applied Malacology in Southeast Asia was established in late 1978 at Mahidol University with an Institution Strengthening Grant from the World Health Organization Special Programme for Research and Training in Tropical Diseases. The long-term objectives of the Center are to: (1) undertake research and training programmes of particular relevance to the region; (2) function as a reference laboratory for snail-host identification and advisory services, as well as maintenance of living and preserved mollusk/parasite stock materials; (3) collaborate closely with and assist in the coordination of other laboratory and field programmes on applied malacology.

The subsidiary long-term objectives of the Center include: (1) the development and standardization of methods, terminology, diagnostic procedures, and field control strategy; (2) the distribution, upon request, of preserved specimens of standard snail-host/parasite strains; (3) the development of training programmes at both professional and sub-professional levels; (4) the preparation, publication and dissemination of information, e.g., scientific journals, manuals, brochures, etc.; (5) the provision of consultant assistance as required.

The Center for Applied Malacology has established an administrative structure and procedures for the operation of the multi-laboratory center; partly trained and up-graded national staff; initiated a reference collection of local snails of medical and socio-economic importance; developed culture methods for the schistosome-bearing snails; and developed a practical and safe snail disposal procedure and containment.

For 1980 and 1981, the Center plans to continue the training and up-grading of the national staff; continue a reference collection of snails; continue culturing snails and maintaining the schistosome cycles; study the distribution, ecology and population dynamics, cytogenetics and electrophoretic characteristics of snails; and study basic aspects of host-parasite relationships. – E.S. UPATHAM

WESTERN SOCIETY OF MALACOLOGISTS. – The 14th Annual Meeting of the Western Society of Malacologists will be held at San Diego State University, San Diego, California, between June 23 and 26, 1981. The meeting will feature symposia and contributed papers on molluscan topics, exhibits, shell and book auction, and field trips. All interested persons are invited to attend. For more information, please contact Bruce Fowler, 5512 Blossom Terrace Ct., San Jose, California 95124, U.S.A.

The Western Society of Malacologists is a non-profit and educational society founded to promote the study of malacology and invertebrate zoology through the encouragement of research, lectures, publications, and acquaintance and cooperation among persons, amateur and professional, interested in these topics.

MALACOLOGICAL REVIEW, SUPPLEMENT 2. – Supplement 2, *The Mekong Schistosome*, J.I. Bruce, S. Sornmani, H.L. Asch & K.A. Crawford, Editors, is now available. This monograph is a compendium of research on a recently described fluke, *Schistosoma mekongi*, which infects humans. This hardbound book contains chapters on such areas as history, epidemiology, life cycle maintenance, susceptibility of intermediate hosts, cercarial emergence, intramolluscan development, morphology, cytogenetics, biochemical genetics, globinase activity, pathobiology, serology, clinical aspects and experimental drug studies, as well as systematics, evolution, bionomics and sensitivity to molluscicides of the unusual snail host, *Tricula aperta*. To order, send US$26.00 per copy (includes postage and handling) to: *Malacological Review*, P.O. Box 420, Whitmore Lake, Michigan 48189, U.S.A.

POSITION IN MALACOLOGY, NATIONAL MUSEUM OF NATURAL HISTORY, SMITHSONIAN INSTITUTION. – The Department of Invertebrate Zoology anticipates a tenure-track oepning on the scientific staff for a freshwater or terrestrial malacologist to function as an associate curator-researcher at the GS-11 level ($20,611). We are particularly interested in all candidates with a Ph.D. and strong background in current systematic biology, molluscan anatomy and evolutionary biology. Send curriculum vitae, copies of publications, and statement of long-term research goals to Dr. Richard S. Houbrick, Search Committee, Department of Invertebrate Zoology, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560, U.S.A. The Smithsonian Institution is an equal opportunity employer.

THE EIGHTH INTERNATIONAL MALACOLOGICAL CONGRESS, sponsored by the Unitas Malacologica, will be held in Budapest, Hungary, in 1983. Further information can be obtained by writing Dr. László Pintér, Unitas Malacologica, c/o Natural History Museum, Baross u. 13, H-1088 Budapest, Hungary.

THE CONCHOLOGICAL SOCIETY OF GREAT BRITAIN AND IRELAND. – The program for the Society for the year 1981 is as follows: *Exhibitions* - Shells from the Indian Ocean (Jan. 17); Fossil cephalopods (Feb. 14); Open exhibition of anything molluscan (Mar. 21); World-wide opisthobranchs (Apr. 11); Gastropoda of temperate waters (May 30); Tropical freshwater bivalves (Oct. 17); Tropical marine bivalves (Nov. 14); Shell artifacts (Dec. 12). *Discussions* - Fred Pinn, 'Shelling in the gulf of Eilat' (Jan. 17); J.H. Callomon, 'No shell like an ammonite' (Feb. 14); J.F.M. de Bartolomé, 'Comments on some Mediterranean rockdwelling helicids' (Mar. 21); Adrian Norris, 'Sylvanus Hanley: an investigation' (Apr. 11); Vera Fretter, 'Factors affecting the reproductive cycle of some gastropods' (May 30); A.J. Brook, 'Algae and freshwater Mollusca' (Oct. 17); John Llewellyn Jones, 'Cockles and mussels alive, alive O!' (Nov. 14); Eleanor Fogan, 'Architectural molluscs' (Dec. 12). *Field meetings* - Camber Sands, East Sussex (May 9); Grand Union Canal (June 6); Hackness, Yorks (June 13); Flitwick Moor, Beds (June 28); West Runton, Norfolk (July 11); Joint meeting with the Northampton Natural History Society (July 26); Pashford Pens Fen, Barton Mills, Suffolk (Sept. 12); Rhossili, Gower (Sept. 19); Autumn slug foray, Midhurst district of the Weald (Oct. 18). Regular meetings of the Society are held in The British Museum (Natural History), Cromwell Road, South Kensington, London, SW7, at 2:30 p.m. in the Demonstration Room.

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CONTENTS OF CURRENT SERIAL PUBLICATIONS ON MOLLUSKS

The contents of current malacological serial publications, as shown by their tables of contents, are herewith reproduced as a service to our readers. The publications are listed in alphabetical order. Also listed are the locations of the editorial offices. Those publications that do not have their contents printed in this current issue of *Malacological Review* are marked by an asterisk in the right hand column below; contents of these publications will be included in future issues of *Malacological Review*.

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By

URIEL N. SAFRIEL, TAMAR FELSENBURG and ANAT GILBOA

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Corpus Christi, Texas

August 5-11, 1979

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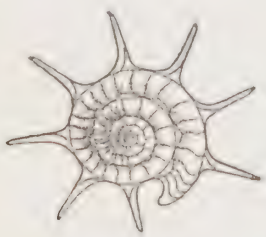

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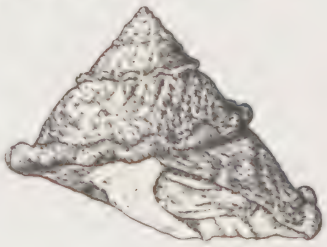

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